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**AN ABSTRACT OF THE THESIS OF**

Sharon Gail London for the degree of Master of Science in Geography presented on February 12, 1999. Title: Spatial Distribution of Understory Vegetation in Tree Canopy Gaps of the Pacific Northwest.

Abstract approved: julia allen jones
Dr. Julia Allen Jones

Understory vegetation in artificially created tree canopy gaps in the Pacific Northwest was studied to determine 1) variation in understory vegetation cover between gap edges and gap centers, as well as between control and treatment plots, 2) spatial patterns of biomass and difference in biomass patterns among plots, 3) individual species responses to gap creation and 4) the relationships between species dominance and diversity by site and treatment. Data were collected in 1990 and 1997 in 16 plots (two controls and two treatments at each of four study sites: the H. J. Andrews Experimental Forest and Martha Creek, Panther Creek, and Trout Creek in the Wind River Experimental Forest). Two of the sites are old-growth stands (250-500 years old), while the other two sites are mature stands (90-150 years old).

Six growing seasons after gap creation, average percent cover of understory vegetation was greater within gaps than at gap edges. Vegetation cover had increased significantly in all artificial gaps, and it had increased more in gaps than in controls. Vegetation cover increased more at Martha Creek, a mature stand, than

at H. J. Andrews and Trout Creek, the two old-growth stands, or at Panther Creek, a mature stand.

Understory biomass increased more in gaps than in controls and the amount of increase varied by site. Initial understory biomass was highest in Panther Creek and Martha Creek, but the magnitude of biomass increase was greatest in Trout Creek and H. J. Andrews. Biomass patterns in 1990 and 1997 were more patchy in old-growth stands than in mature stands.

Vegetation cover of most understory species increased from 1990 to 1997 in artificial gaps, but species' responses were often site specific. In some cases, species with advantageous dispersal mechanisms (such as rhizomes, stolons, or clonal growth, e.g. *Rubus ursinus,* or *Acer cinncinatum*) increased in cover and biomass more than species without such advantageous dispersal mechanisms. Cover of weedy species such as *Epilobium angustifolium* and *Lactuca muralis* increased dramatically (up to 25 times) in artificial gaps, but weedy species represented less than two percent of the total average cover in 1997.

Species dominance and diversity did not respond consistently following gap creation. Species dominance was relatively high (species with highest dominance was 30 $g/m^2$) and diversity relatively low (38 species) at Martha Creek, a mature stand, whereas species dominance was low and diversity high at H. J. Andrews (9 $g/m^2$, 51 species), an old-growth site. Panther Creek, a mature stand, and Trout Creek, an old growth stand, had intermediate dominance and high diversity (17 $g/m^2$, 57 species at Panther Creek and 18 $g/m^2$, 41 species at Trout Creek).

# Spatial Distribution of Understory Vegetation in Tree Canopy Gaps of the Pacific Northwest

by

Sharon Gail London

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Sharon G. London

Sharon Gail London, Author

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**Spatial Distribution of Understory Vegetation in Tree Canopy Gaps of the Pacific Northwest**

# 1. INTRODUCTION

Tree canopy gaps are important to the species dynamics of forest types around the world (Pickett and White 1985, Platt and Strong 1989). Gaps are naturally formed openings in a forest canopy that form due to the death of one or more trees. Dead trees remain as snags or fall and become nurse logs composed of organic matter essential for nutrient cycling (Franklin and Harmon 1987). Resources such as light and moisture tend to be more abundant in gaps than in surrounding forests (Canham and Marks 1985), which also encourages tree seedling and understory growth (Veblen 1992).

Most studies of gap dynamics have focused on responses of dominant (tree) species to changes in resource availability, particularly in eastern United States and in tropical forests (Runkle 1982, Canham 1993, Denslow 1987, Uhl *et al.* 1988, Bazzaz and Wayne 1994). More recent gap studies in the Pacific Northwest also focus primarily on tree species (Spies *et al.* 1990, Gray 1995, Gray and Spies 1997). Trees are usually the focal species as they are larger and have more commercial value than shrubs and herbs.

Comparatively little attention has been focused on gap dynamics of understory vegetation in the Pacific Northwest, although a few studies have looked at understory vegetation in Northeast United States hardwood forests (Beatty 1984,

Collins and Pickett 1988, Goldblum 1997). In mature forests and old-growth forests of the Pacific Northwest, understory vegetation dynamics in gaps are important for a number of reasons. Gaps are areas of high plant diversity and play an important ecological role of supporting much of floristic and fauna diversity (indirectly or directly), especially in old-growth forests (Halpern and Spies 1995). Understory shrubs are a major component of wildlife habitat (Bailey and Tappeiner 1998) and understory shrubs and herbs may provide both food and habitat for numerous animals such as deer, elk, birds, and rodents.

Numerous studies have found that vascular plant richness in Pacific Northwest forest resides primarily within the shrub and herbaceous layers (Bailey *et al.* 1998). Although few understory species are restricted from or absent from any stage of stand development, many species differ in abundance among stages. Vascular plant diversity is greatest in old-growth forests and many species are more abundant in old-growth forests (Halpern and Spies 1995, Spies 191).

In addition, tree gaps are important as transition areas from mature forests to old-growth forests (Spies and Franklin 1989). Vegetation response to gaps may be largely determined by vegetation patterns that are established in the understory of closed canopy forests (Brokaw and Scheinter 1989).

Understory vegetation also is important for the hydrologic cycle. Water is especially important during the summer months for understory vegetation in Pacific Northwest forests, and the rapid growth of understory vegetation appears to influence summer stream flows (Bredensteiner 1998). Soil moisture is often higher

in gaps than closed canopy areas, with decreasing levels near gap edges (Denslow 1987). The increased moisture levels in gaps compared to surrounding forested areas may be due to less water use by transpiring vegetation (Veblen 1992), lower root density and/or more precipitation reaching the ground (Canham 1993).

Understory vegetation dynamics are especially important since understory vegetation can limit tree seedling establishment and growth (Veblen 1992), as well as encourage growth for some tree seedlings. Gray (1995) found that understory vegetation reduced tree seedling establishment in closed-canopy areas and shaded areas of gaps in the Pacific Northwest.

To further understand understory vegetation dynamics in tree gaps and the effect of gaps on understory vegetation in the Pacific Northwest, three major objectives were addressed in this study. First, to partially capture the effects of within-site variability in light and moisture, understory vegetation abundance at the centers of gaps was contrasted with understory vegetation abundance at gap edges. Second, the overall effect of treatment (gap creation) on percent average cover and biomass of understory vegetation was examined. Finally, since interactions between species may significantly affect dominant tree species, the effect of treatment on selected species was addressed, as well as the question of species dominance and diversity.

# METHODS

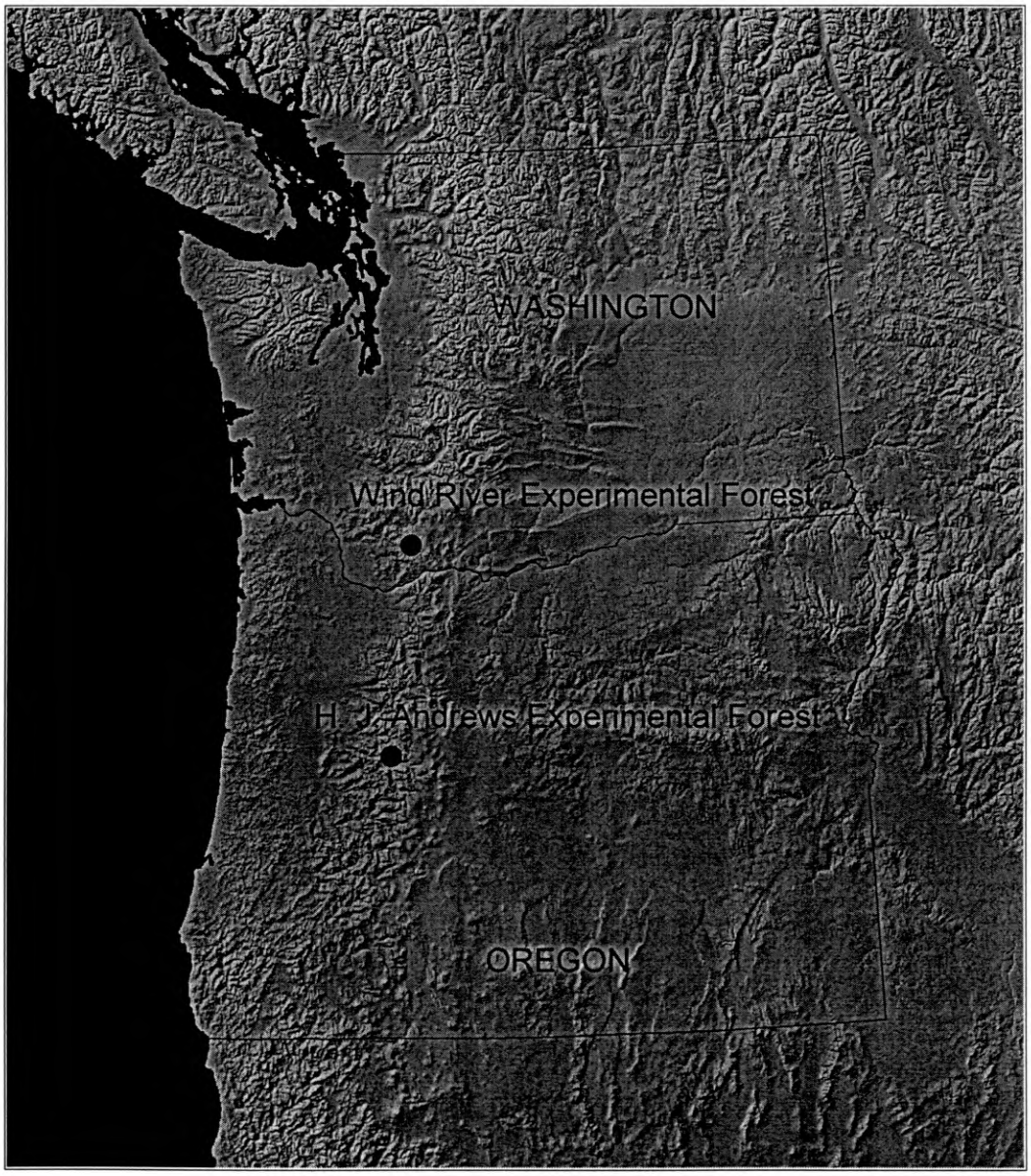
## 2.1 Study Site Description

One stand is located in the H.J. Andrews Experimental Forest in the Willamette National Forest, while the other three stands are located in the Wind River Experimental Forest in the Gifford-Pinchot National Forest (Figure 1). The three sites located in the Wind River Experimental Forest are Trout Creek (45°49' N, 122°00' W), Panther Creek (45°50' N, 121°49' W) and Martha Creek (45°47' N, 121°57 W). The site at the H.J. Andrews Experimental Forest is McRae Creek (44°15' N, 122°15' W).

All four study sites are found in the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973) of the west slope of the Cascade Mountains. H. J. Andrews and Trout Creek are in old-growth forests (approximately 500 years in age) with *Pseudotsuga menziesii* and *Tsuga heterophylla* as dominant trees in multi-canopy layers with dominant understory species including *Berberis nervosa*. Martha Creek and Panther Creek are in mature forests (90-140 years in age) dominated by *P. menziesii* in a single canopy layer with dominant understory species including *Gaultheria shallon*, *Berberis nervosa* and *Acer cinncinatum* (Gray 1995).

Disturbance history varies among the four sites. McRae Creek, at H.J. Andrews, is an old-growth site where a fire of moderate severity occurred 140 years ago (Teensma 1987). A dense sub-canopy of *Tsuga heterophylla* followed this disturbance, which may have reduced the amount of understory vegetation

Figure 1: Study Sites are located in the Cascade Mountain Range of the Pacific Northwest. One stand, McRae Creek, is located at the H.J. Andrews Experimental Forest in Central Oregon, while the other three stands (Trout Creek, Martha Creek and Panther Creek) are located in the Wind River Experimental Forest in Southern Washington (source: Oregon State Service Center for GIS).



(Gray 1995). The other old-growth site, Trout Creek, had patchy canopy cover and understory density of varying amounts. It had no obvious signs of disturbance other than small patches of canopy mortality (Gray 1995). Martha Creek is a mature stand established after the Yacolt fire of 1902 (Hofmann 1917) and it is dominated by *Pseudotsuga menziesii* (Douglas-fir) in the overstory, *Acer cinncinatum* (vine maple) in the mid-story and woody shrubs in the understory. Most of the large snags appear to have been cut in the 1930's, most likely to discourage the spread of fire (Gray 1995). Panther Creek, the other mature stand, has experienced at least one severe *Dendroctomus pseudotsugae* (Douglas-fir beetle) outbreak and was salvage-logged in the 1950's. The canopy in Panther Creek was fairly open and had a high density of vine maple, herbs and shrubs (Gray 1995). Coarse woody debris cover and decomposition rates were greater in the old-growth sites (approximately 40% cover at H. J. Andrews and 44% cover at Trout Creek), than the mature sites (approximately 31% cover at Martha Creek and 11% cover at Panther Creek) (Gray 1995).

Soils in the four stands are weakly developed and vary in texture. H.J. Andrews is a deep (depth to C horizon 1 m), well-drained, dark brown gravelly loam over a cobbly silt loam C horizon. It was formed in colluvium from basic igneous rock and volcanic ash, and is classified as a loamy skeletal, mixed, frigid Fluventic Dystrochrept (Brown 1975, Gray 1995). Trout Creek is a deep (typically two meters to bedrock) well-drained, dark brown sandy loam soil and was formed in relatively young deposits of volcanic tephra over basaltic lava flows. It is

classified as an Andic Haplumbrept belonging to the Stabler series (Franklin and DeBell 1988, Gray 1995). Soil classifications for the two mature stands were unavailable, though Gray (1995) derived textural classes from particle size analyses of clay loam for Martha Creek and sandy loam for Panther Creek.

The elevation of all four stands ranges from 550 m at Trout Creek and Martha Creek, to 850 m at Martha Creek and 900 m at H.J. Andrews (Table 1). Plots were located in areas with slopes less than 20%, where vegetation was similar, and tree canopies were fairly dense, in order to minimize interactions with other disturbances (Gray 1995).

The climates at both H.J. Andrews and Wind River are fairly similar with summer droughts from June to September and high temperatures around 21°C at the Wind River to 27°C at the H.J. Andrews. The sites are all located in the transient snow zone, with ephemeral snowpacks up to one meter. Average yearly precipitation, based on 30 year records, was 2200 millimeters at a low elevation site at H.J. Andrews (data taken from the H. J. Andrews Watershed 2 meteorological station), compared to 2692 millimeters at a low elevation at the Wind River (WRCC 1999). Winter precipitation is slightly greater at Wind River than H. J. Andrews, while H. J. Andrews precipitation is greater than Wind River in the spring and late fall.

Soil moisture levels tended to be higher in old-growth plots than mature plots, possibly due to environmental variables such as soil, understory vegetation density or topography (Gray 1995). Light levels in control plots were highest at

**Table 1:** Description of four treated-control paired replicates of tree canopy gaps in the western Cascades of Oregon and Washington (from Gray 1995).

| site | reference code | location | size (ha) | elevation (m) | slope | soil texture |
|---|---|---|---|---|---|---|
| *H.J. Andrews Experimental Forest* | | | | | | |
| McCrae Creek | HJA | 44°15' N, 122°15'W | 0.28 | 900 | <20% | loam |
| *Wind River Experimental Forest* | | | | | | |
| Martha Creek | MCY | 45°47' N, 121°57' W | 0.18 | 550 | <20% | clay, loam |
| Panther Creek | PCM | 45°50' N, 121°49' W | 0.28 | 850 | <20% | sandy loam |
| Trout Creek | TCO | 45°49' N, 122°00' W | 0.36 | 550 | <20% | loam |

Panther Creek, intermediate at Trout Creek and Martha Creek and lowest at H.J. Andrews. The light levels in the gaps were more variable and could not be easily ranked by stand, possibly due to crown outline differences at southern edges of gaps (Gray 1995). In addition, in 1992 patterns were evident of increasing light levels from the southern to the northern edge of gaps (Gray 1995).

## 2.2 Experimental Design

This understory vegetation study is part of a larger study on ecosystem processes within gaps. The long-term study began in 1990 and compares different size gaps as well as other ecosystem processes, such as tree seedling establishment (Gray and Spies 1996, Gray 1995). In the summer of 1990, pre-treatment data were collected in both control and treated sites. In the fall of 1990, trees over two meters tall were cut within specified boundaries to create gaps of different sizes. To avoid damage to southern trees, trees were stage-felled into the northeast and/or northwest quadrants, which defined the gap shade pattern. In order to minimize disturbance to soils and understory vegetation, skidders were situated outside of the gaps. Fallen tree boles were winched from the gaps with cables, while branches and foliage trimmed from the felled trees were placed outside the gap perimeter to avoid localized differences in nutrient input and shading within the gaps (Gray 1995). This study only deals with the largest gap diameter which is the equivalent of a single tree height (~ 60 m).

Within each of the four sites described above, there are four circular plots: two controls and two treatments (gaps), each approximately 0.25 ha in area (Figure 2). The area inside a gap plot is defined as a gap center, whereas the area outside the boundary of the forest canopy is called a gap edge. Edges usually have forest cover compared to gap centers, which are exposed and have more light.

## 2.3 Sampling Design and Data Collection

Data were collected in the summers of 1990 (approximately three months before gap creation) and 1997 (seven years after gap creation). Within each plot, permanent markers (PVC pipe) were surveyed prior to gap creation at a 2 meter spacing on the north-south and east-west axes of all gaps, and at a 4 meter spacing in all primary (100 and 110) gaps. Secondary (200 and 210) gaps were sampled at a 4-meter spacing only along 45-degree diagonals. Nested vegetation sampling areas 0.25 $m^2$ in size, centered on the permanent markers, were used to calculate percent cover and biomass. Although two levels of sampling were conducted (0.25 $m^2$ and 3.14 $m^2$), only the smaller size data points were used in this analysis.

Ocular estimates were made of percent cover for every understory species. The field crew calibrated estimations throughout the field season to reduce error. Every vegetation sampling point in a plot was sampled (Table 2), all species present were listed, and percent cover for a 0.25 $m^2$ data point was assigned for each species using a vertical projection method. All trees with diameter at breast

Figure 2: Theoretical study site (box border) composed of four plots: two controls (100 and 200) and two treatments (110 and 210). The primary plots were sampled more extensively than the secondary plots.

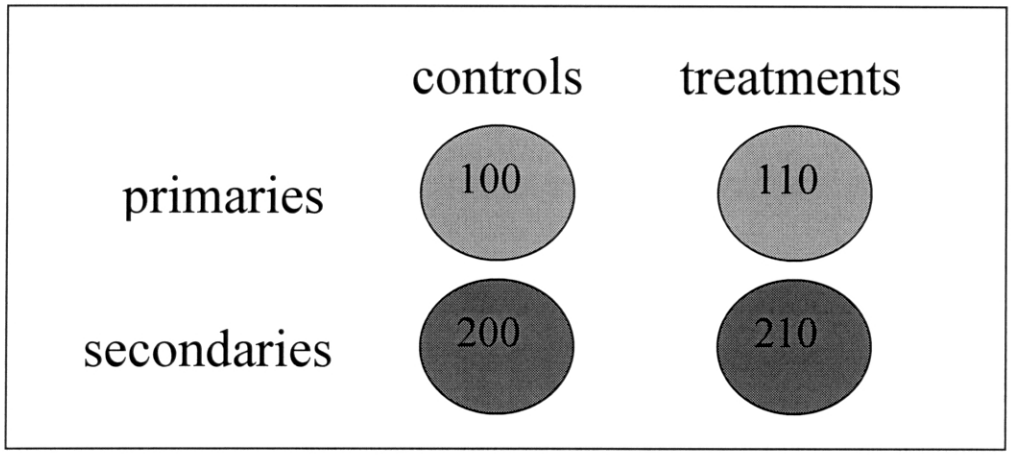


**Table 2:** Description of four treated-control paired replicates of tree canopy gaps in the western Cascades of Oregon and Washington. Site information, number of data points and number of species occurrence by study plot and year (out of possible 115 species).

| SITES | | | | | DATA POINTS (pts) | | | SPECIES (spp) | |
|---|---|---|---|---|---|---|---|---|---|
| site | reference code | treatment/ control | primary/ secondary | old-growth/ mature | n (# pts) | n-gap* (# pts) | n-edge* (# pts) | 1990** (# spp) | 1997 (# spp) |
| *H.J. Andrews Experimental Forest* | | | | | | | | | |
| McCrae Creek | HJA100 | c | p | old-growth | 197 | n/a | n/a | 31 | 36 |
| McCrae Creek | HJA110 | t | p | old-growth | 224 | 142 | 82 | 37 | 61 |
| McCrae Creek | HJA200 | c | s | old-growth | 77 | n/a | n/a | 29 | 24 |
| McCrae Creek | HJA210 | t | s | old-growth | 87 | 65 | 22 | 25 | 45 |
| *Wind River Experimental Forest* | | | | | | | | | |
| Martha Creek | MCY100 | c | p | mature | 121 | n/a | n/a | 28 | 28 |
| Martha Creek | MCY110 | t | p | mature | 148 | 89 | 59 | 18 | 48 |
| Martha Creek | MCY200 | c | s | mature | 57 | n/a | n/a | 14 | 15 |
| Martha Creek | MCY210 | t | s | mature | 66 | 48 | 18 | 23 | 42 |
| Panther Creek | PCM100 | c | p | mature | 205 | n/a | n/a | 54 | 52 |
| Panther Creek | PCM110 | t | p | mature | 200 | 123 | 77 | 54 | 63 |
| Panther Creek | PCM200 | c | s | mature | 77 | n/a | n/a | 37 | 39 |
| Panther Creek | PCM210 | t | s | mature | 91 | 67 | 24 | 45 | 59 |
| Trout Creek | TCO100 | c | p | old-growth | 205 | n/a | n/a | 26 | 25 |
| Trout Creek | TCO110 | t | p | old-growth | 234 | 135 | 99 | 35 | 48 |
| Trout Creek | TCO200 | c | s | old-growth | 73 | n/a | n/a | 24 | 28 |
| Trout Creek | TCO210 | t | s | old-growth | 89 | 62 | 27 | 26 | 33 |

* Controls do not have gaps or edges so the number of plots is not applicable (n/a).

** 1991 data used for HJA100 since 1990 data had errors.

height (dbh) greater than five centimeters were tagged and measured (Figures 3a, 3b). In 1992, gap edges were mapped for all treated plots by drawing the tree canopy boundaries (Figures 4a-h).

Biomass was calculated for selected weedy and thick stemmed species such as fireweed (*Epilobium angustifolium)* and vine-maple (*Acer cinncinatum*) and tree seedlings, by taking basal diameters using calipers. The total number of species per vegetation data point was also tallied. Like, percent cover estimates, biomass data were collected for both small and large sampling points, but only the small sampling point data excluding tree seedlings were used in this analysis.

## 2.4 Target Species

This analysis focused only on understory vegetation (shrubs and herbs) and did not include trees or tree seedlings (see Gray 1995 for seedling information). As there are over 115 species in the four stands, 12 representative species were selected. These species were selected on the basis of abundance, dispersal and ecological importance (such as species indicative of old-growth forests or species common in all stands).

Table 3 shows the 12 species chosen to represent understory vegetation. There are five herbs, two of which are weedy, and seven shrubs. Most species are well dispersed, such as Pacific *Rubus ursinus* (blackberry), which is common throughout all the plots and especially abundant after disturbance. *Rhododendron*

Figure 3a: Map of tree stems at the control study site at Trout Creek, an old-growth stand. Abbreviations are: 'ABAM' = *Abies amabilis*, 'ABPR' = *Abies procera*, 'PSME' = *Pseudotsuga menziesii*, 'TABR' = *Taxus brevifolia,* and 'TSHE' = *Tsuga heterophylla.i*

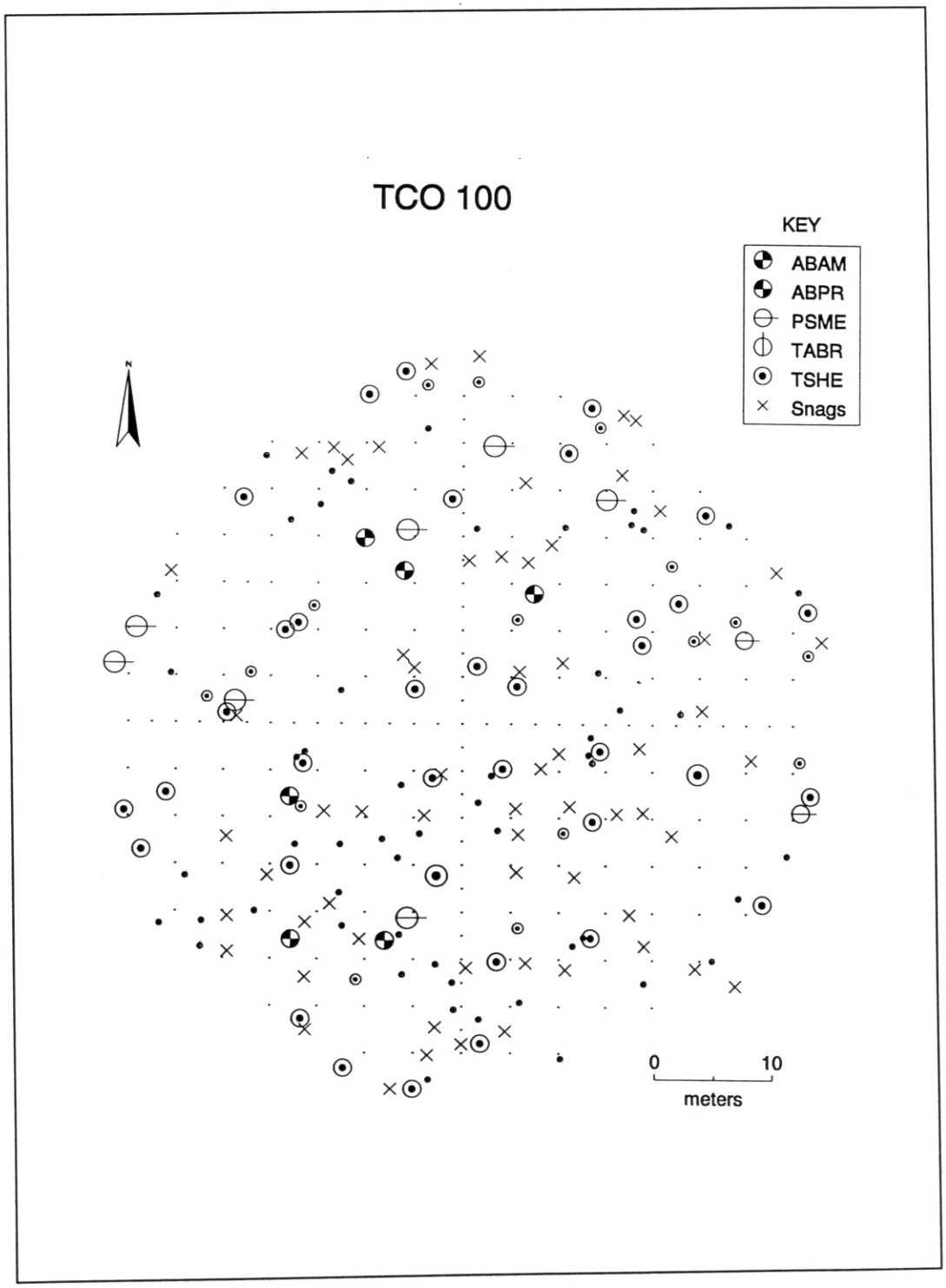


Figure 3b: Map of tree stems at the primary control study site at Panther Creek, a mature stand. Abbreviations are: This site is dominated by *Pseudotsuga menziesii* (PSME), and *Cornus nutalii* (CONU).

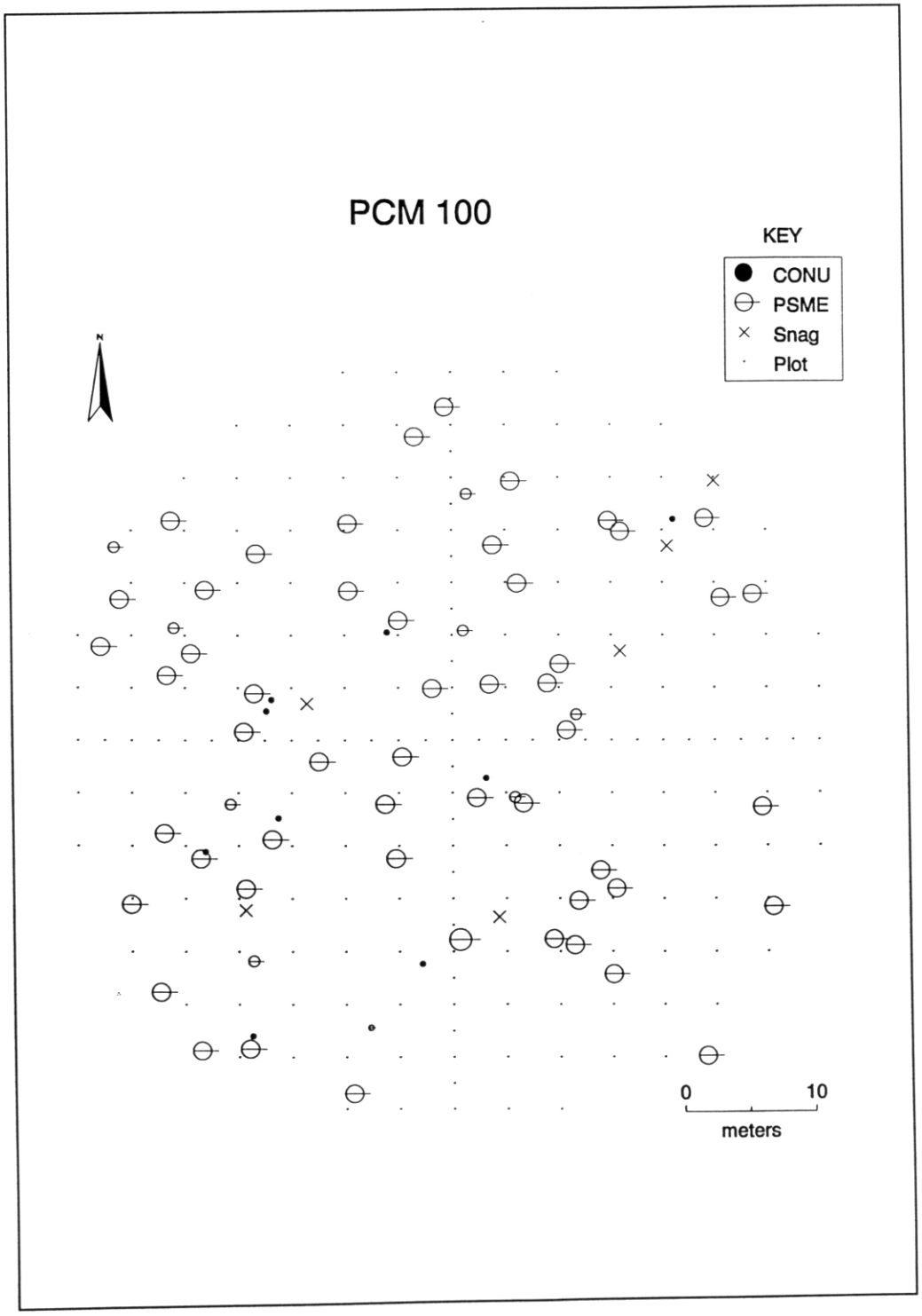


**Table 3:** 12 target species used in this study and their dispersal mechanisms (from Hitchcock and Cronquist, 1973).

| Code | Genera and Species | Common Name | Family | Primary Dispersal Mechanism |
|---|---|---|---|---|
| Herbs | | | | |
| ACTR | *Achlys triphylla* | vanilla leaf | Beberidaceae | rhizomatous |
| COCA | *Cornus canadensis* | bunchberry | Cornaceae | seeded |
| EPAN | *Epilobium angustifolium* | fireweed | Onagraceae | rhizomatous |
| LAMU | *Lactuca muralis* | wall lettuce | Compositae | wind-dispersed |
| LIBO2 | *Linnaea borealis* | western twinflower | Caprifoliaceae | clonal and rhizomatous |
| Shrubs | | | | |
| ACCI | *Acer cincinatum* | vine maple | Aceraceae | layering and sprouting; clonal |
| BENE | *Berberis nervosa* | Oregon grape | Beberidaceae | seeded |
| GASH | *Gaultheria shallon* | salal | Ericaceae | clonal and rhizomatous |
| RHMA | *Rhododendron macrophyllum* | Rhododendron | Ericaceae | seeded |
| ROGY | *Rosa gymnocarpa* | baldhip rose | Rosaceae | seeded |
| RUUR | *Rubus ursinus* | Pacific blackberry | Rosaceae | trailing and rhizomatous |
| VAPA | *Vaccinium parvifolium* | red blueberry | Ericaceae | seeded |

*macrophyllum* (Rhododendron), however, is only found at H.J. Andrews and an example of a poorly dispersed species. Shrubs with advantageous dispersal mechanisms (such as clonal sprouting, rhizomes or stolons) include *Acer cinncinatum* (vine maple), *Gaultheria shallon* (salal) and *Rubus ursinus* (Pacific blackberry). *Lactuca muralis* (wall lettuce) and *Epilobium angustifolium* (fireweed), the two weedy species, are both wind-dispersed. *Berberis nervosa* (Oregon grape), *Vaccinium parvifolium* (red blueberry), and *Rosa gymnocarpa* (bald-hip rose) are shrubs common in old-growth stands and mature stands, while *Achlys triphylla* (vanilla leaf), *Linnaea borealis* (western twinflower), and *Cornus canadensis* (bunchberry) are common herbs (Spies and Franklin 1989).

## 2.5 Hypotheses

Because gap centers show increases of light and soil moisture (Gray 1995), the first part of the analysis tested the hypothesis that gap creation (treatment) will increase average percent cover of understory vegetation in gap centers compared to gap edges.

The second part of the analysis was to test the interactive effects of site (location and plot age) and experimental treatment (gap or control) on changes in vegetation cover and biomass from 1990 to 1997. Because many understory species may be light-limited due to tree-canopy cover, it was hypothesized that vegetation cover and biomass would increase more in gaps than in controls, and would

increase more in gaps located in mature stands than in gaps found in old-growth stands.

The third part of the analysis tested the hypothesis that there is a biological legacy of understory species. It was hypothesized that vegetation cover of most species would increase with gap creation due to greater availability of resources such as light and moisture. It was expected that species with advantageous dispersal mechanisms (such as rhizomes, stolons, or clonal growth) to increase in cover and biomass more than seed dispersed species. It was also expected weedy species to increase more in treatments than in controls. In addition, species' dominance was expected to be greatest in mature stands, and species' diversity was expected to be greatest in old-growth stands.

## 2.6 Data Analysis

For the edge analysis, eight gaps were analyzed (two replicates at each of the four sites). Control plots were not used as there are no gaps or edges. Gap centers were then differentiated from gap edges by overlaying gap outline maps (Figures 4a-h) on plot maps and extracting all points outside of the canopy outline to form the "edge," and all points inside the canopy boundary to form the "gap". Data from both 1990 (before gap creation) and 1997 (after gap creation) were included. Average percent cover for gaps and edges was derived by summing the total percent cover for each of the 12 species of interest at each data point, adding

Figure 4a: Map of H.J. Andrews primary treatment site showing sampling points in gap centers and sampling points in gap edges.

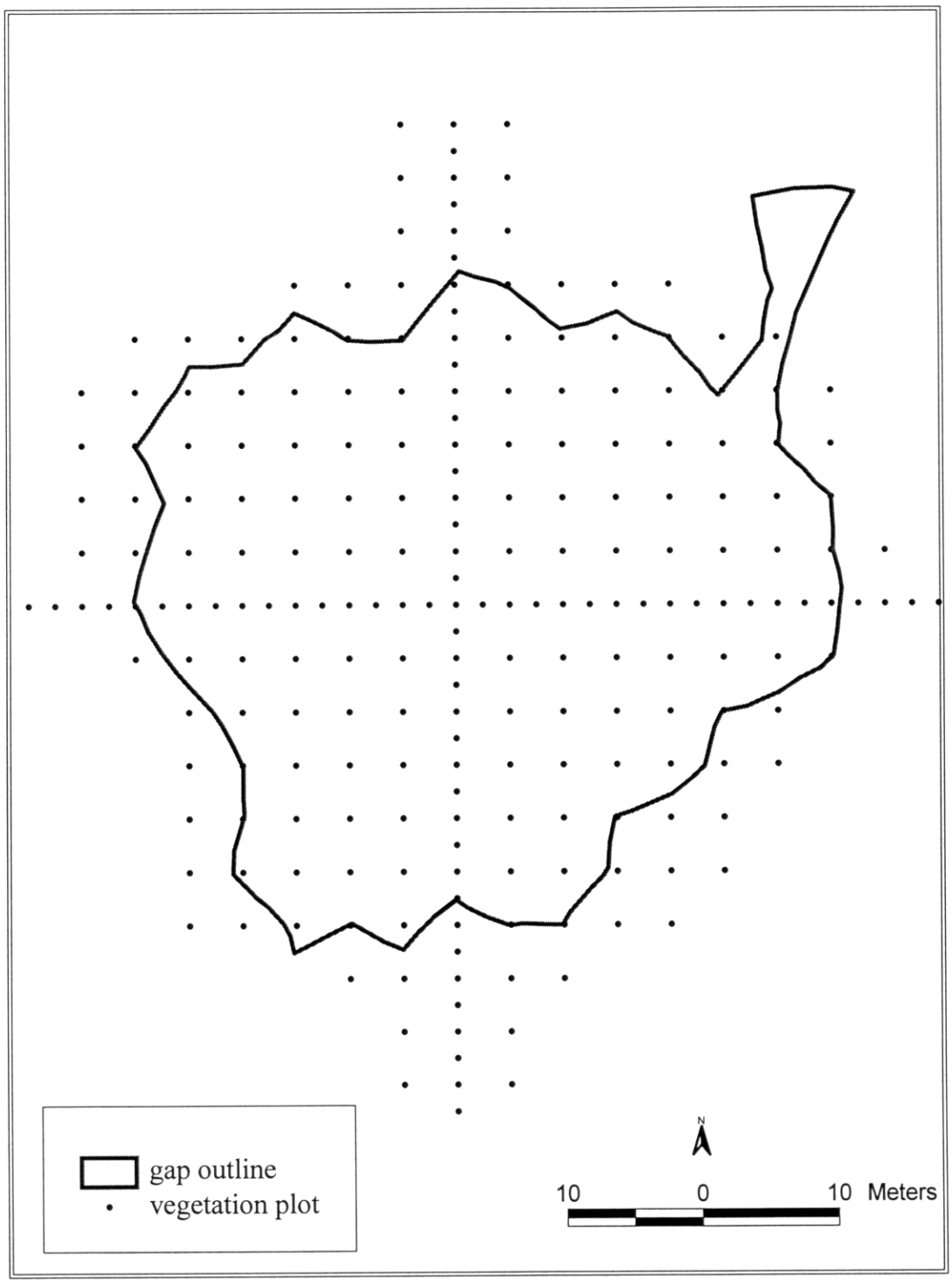


Figure 4b: Map of H.J. Andrews secondary treatment site showing sampling points in gap centers and sampling points in gap edges.

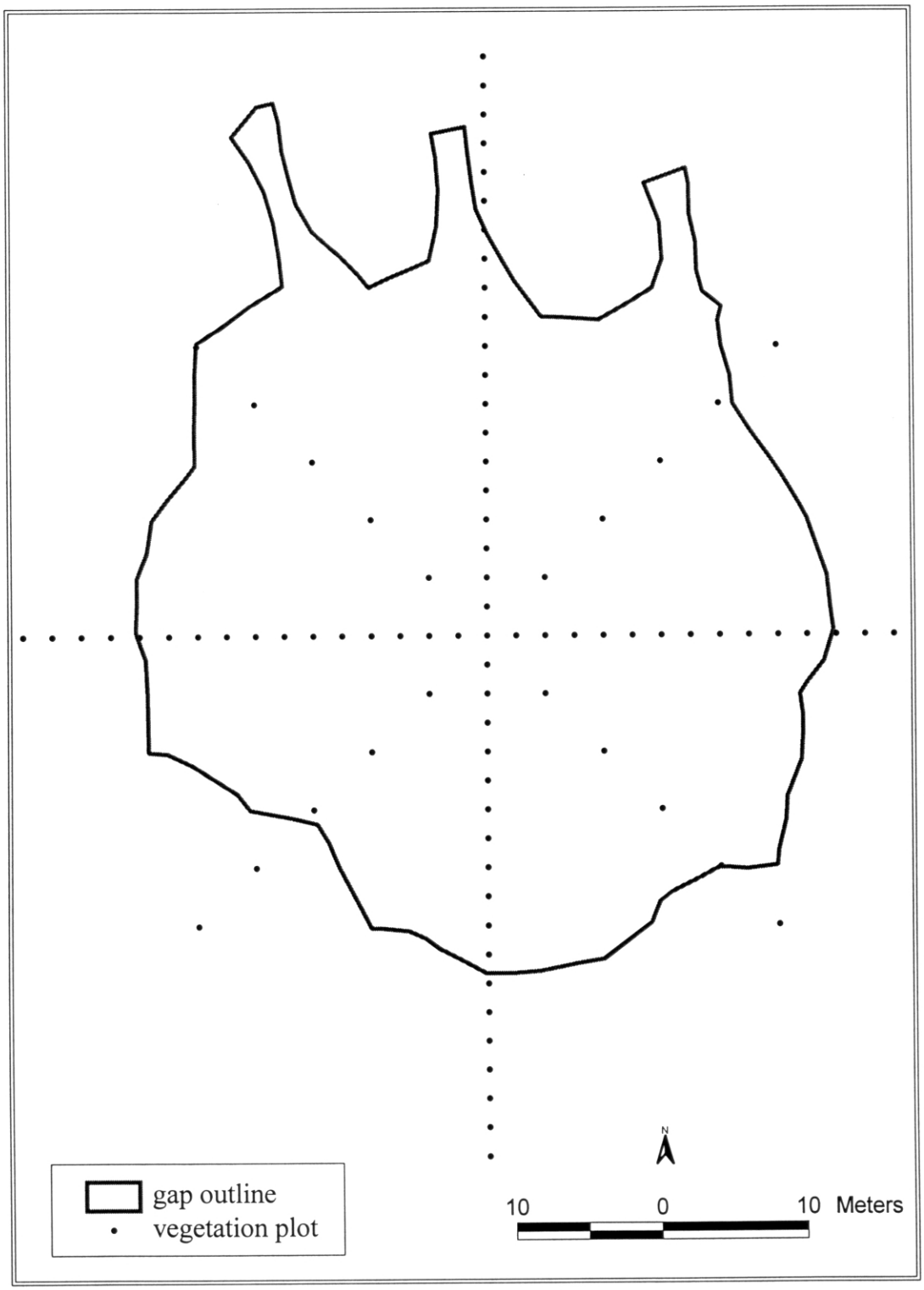


Figure 4c: Map of Martha Creek primary treatment site showing sampling points in gap centers and sampling points in gap edges.

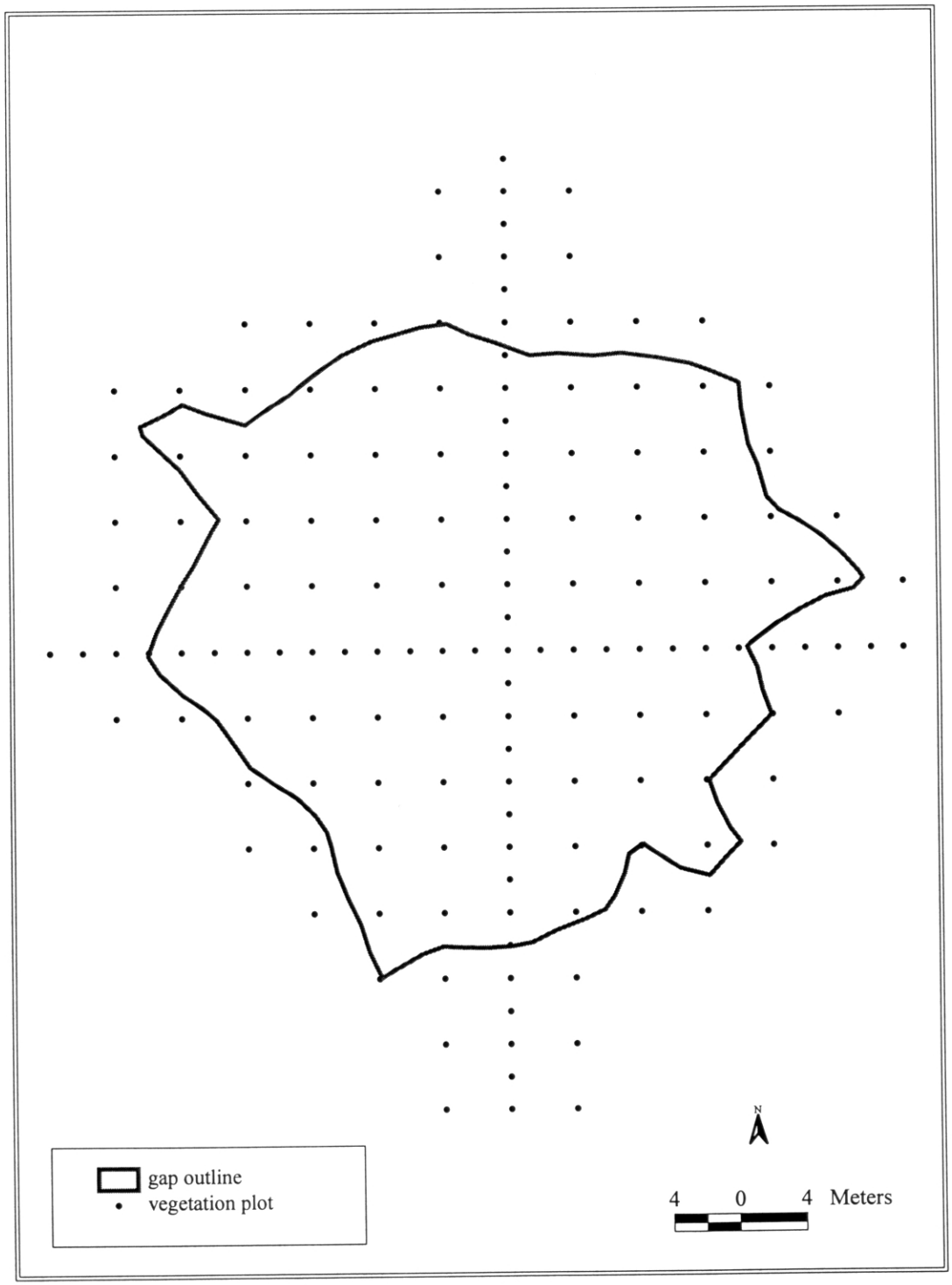


Figure 4d: Map of Martha Creek secondary treatment site showing sampling points in gap centers and sampling points in gap edges.

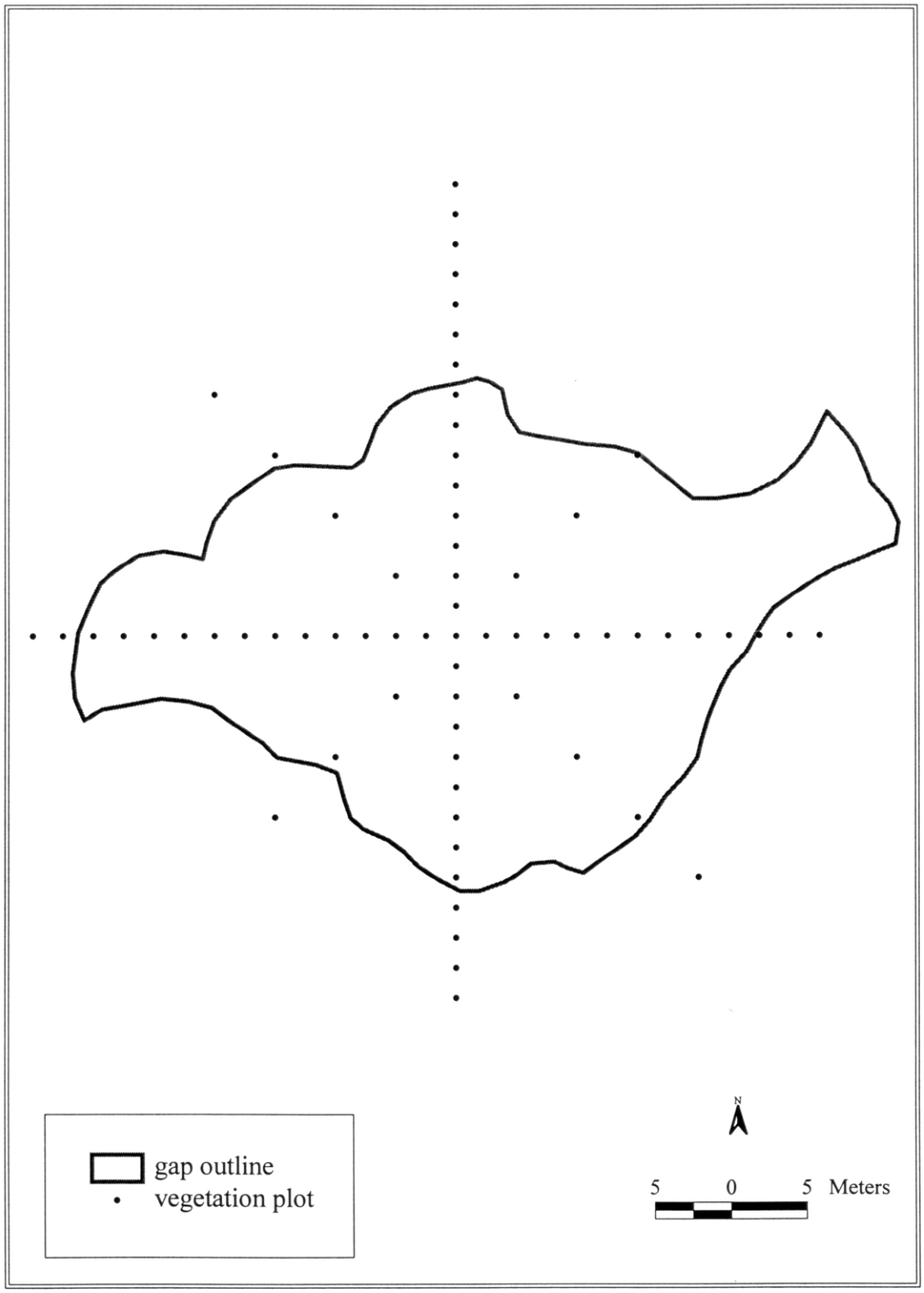


Figure 4e: Map of Panther Creek primary treatment site showing sampling points in gap centers and sampling points in gap edges.

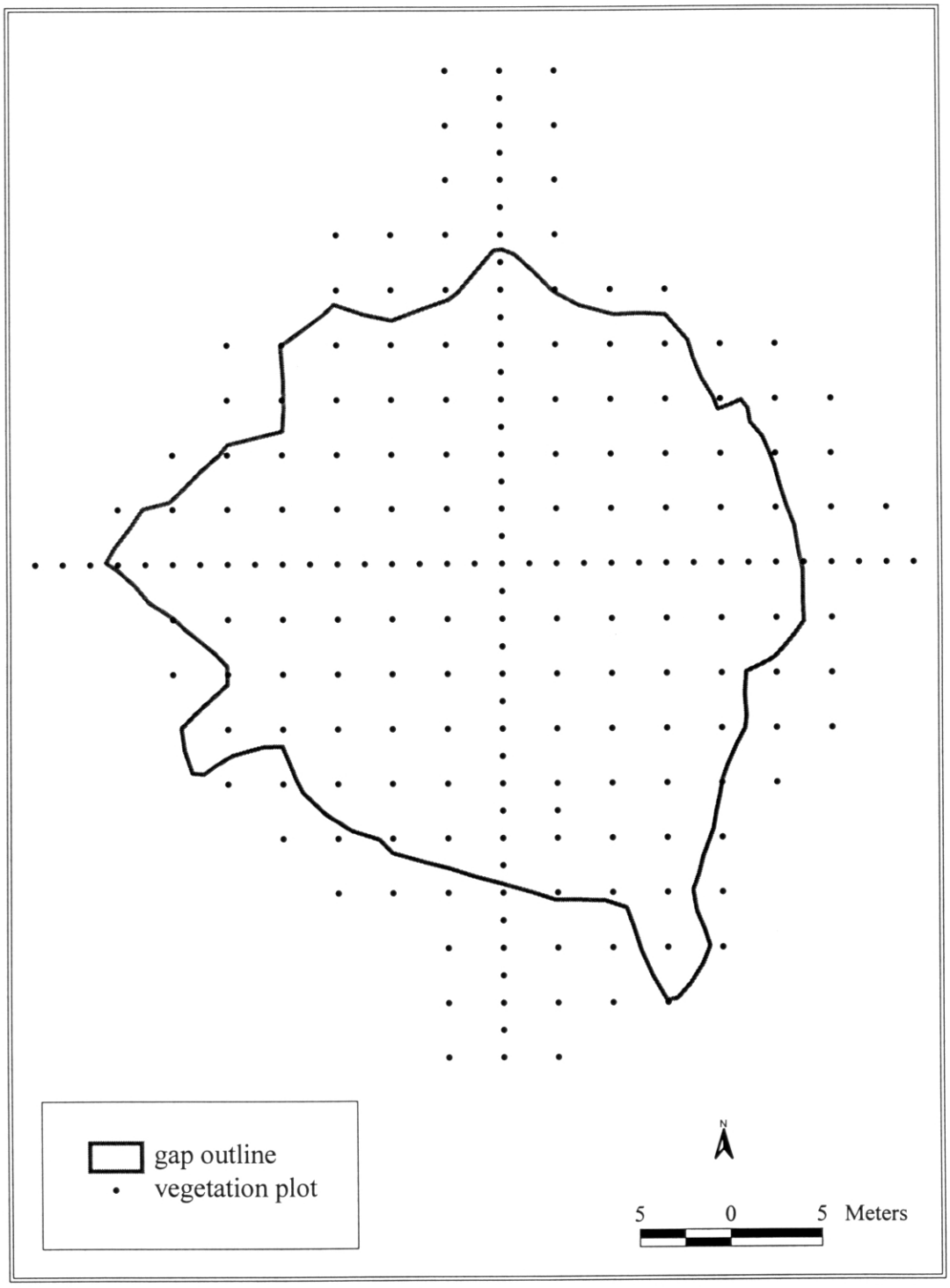


Figure 4f: Map of Panther Creek secondary treatment site showing sampling points in gap centers and sampling points in gap edges.

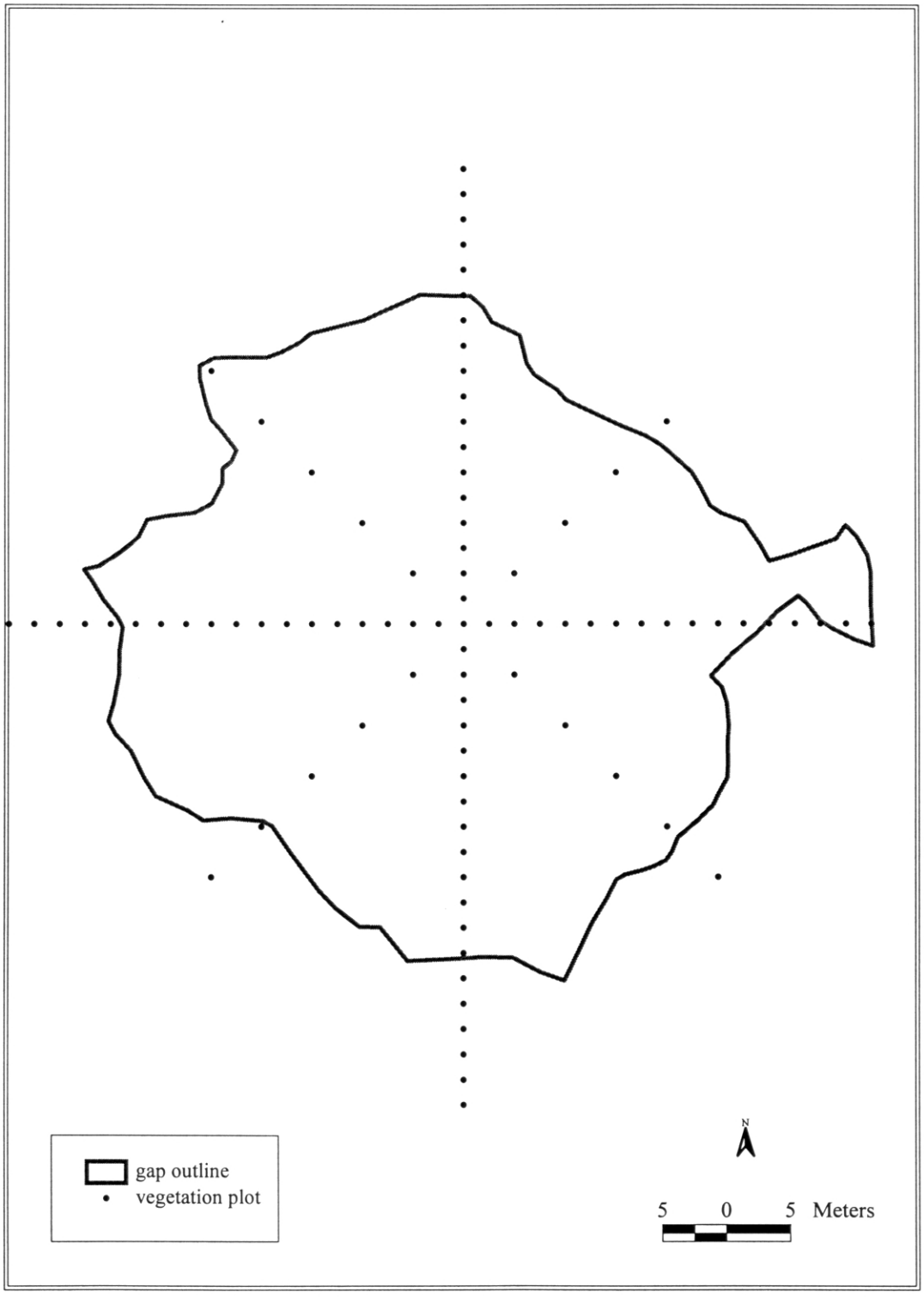


Figure 4g: Map of Trout Creek primary treatment site showing sampling points in gap centers and sampling points in gap edges.

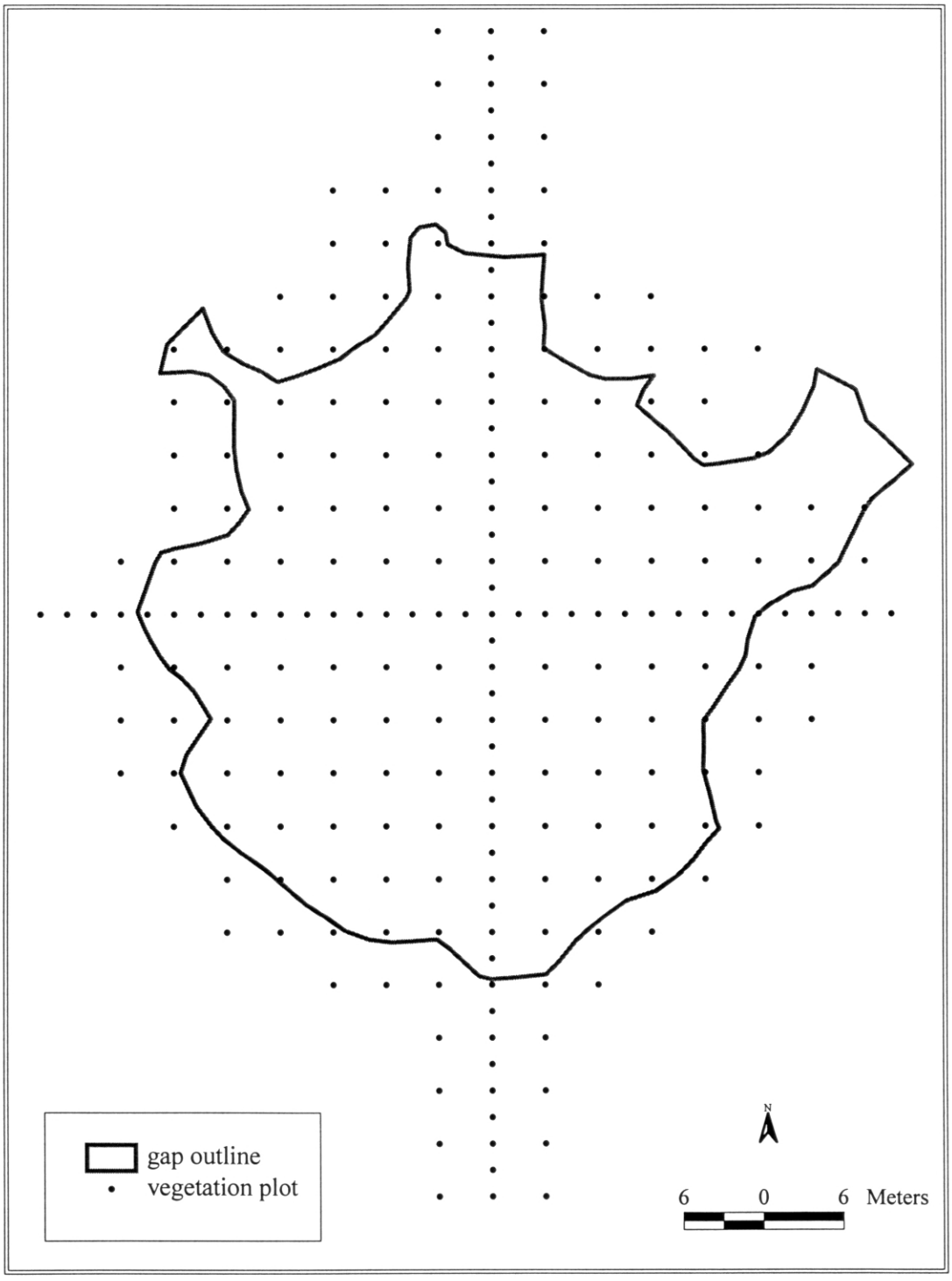
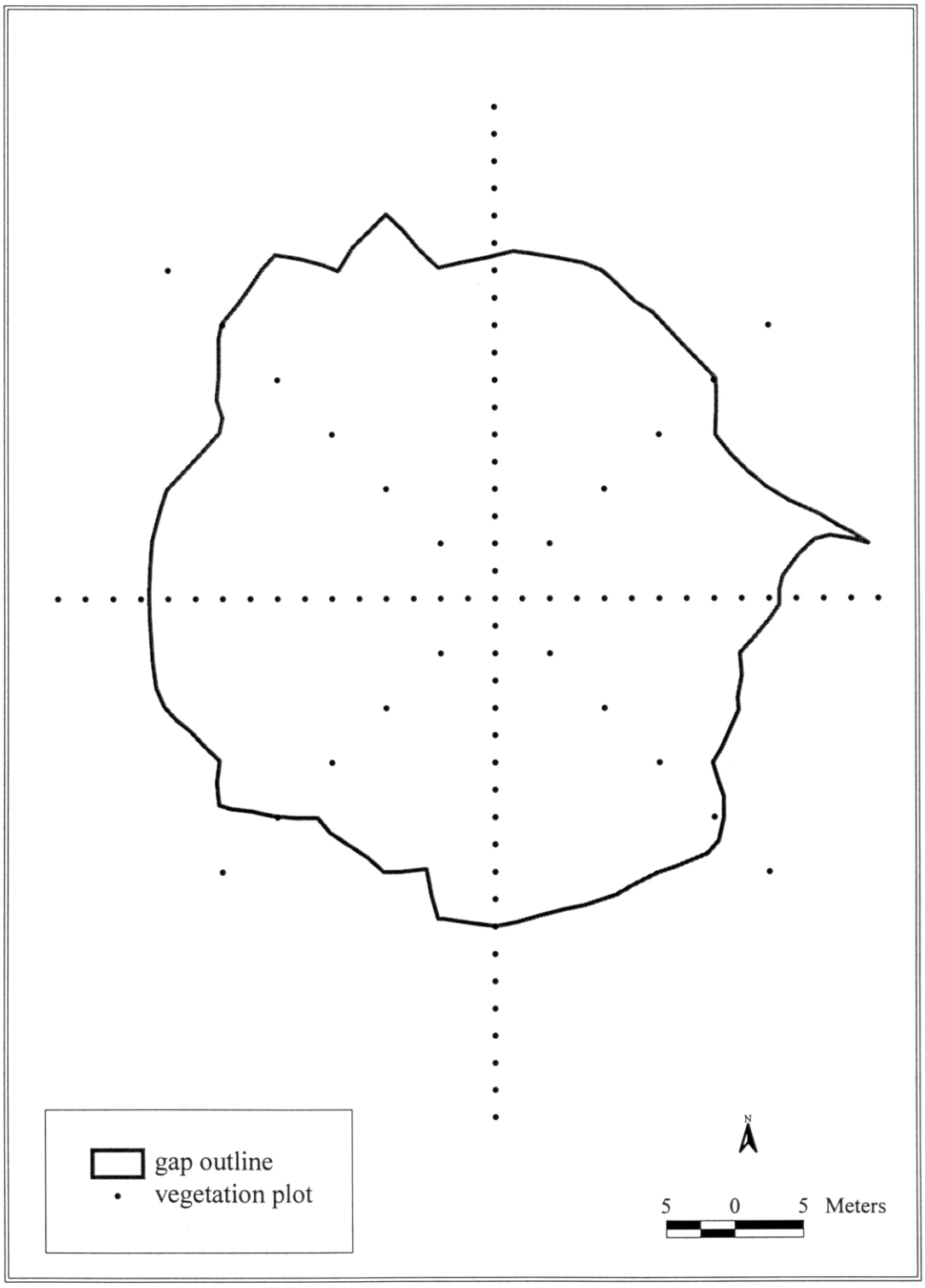


Figure 4h: Map of Trout Creek secondary treatment site showing sampling points in gap centers and sampling points in gap edges.



the totals for all data points, and dividing by the number of data points in a gap or along an edge. Positive values indicate an increase in cover, while negative values indicate a decrease in cover from 1990 to 1997. The formulas used were:

Percent cover: $c_{ijt}$ = % cover per data points (j) of species i, year t

Where:

i = 1……..m (12 target species- 115 total species)

j = 1 ……..n (data points per plot, varied by site [Table 2])

t = 1, 2 (1 =1990, 2 = 1997)

dif = difference

Average cover per data point of 12 target species, year 1:

$$\overline{C_1} = \frac{\sum_{i=1}^{12} \sum_{j=1}^{n} c_{ij1}}{n}$$

Average percent difference (relative change) in cover 1990-1997, per data point of 12 target species:

$$\text{dif } C_i = \overline{C}_{j2} - \overline{C}_{j1}$$

Absolute change in percent average cover 1990-1997, per data point of 12 target species:

$$\Delta C_i = 100 * \frac{\overline{C}_{ij2} - \overline{C}_{ij1}}{\overline{C}_{ij1}}$$

For percent vegetation cover analysis, both treatments (gaps) and controls (16 plots composed of two controls, two treatments per study site) were compared. Percent average cover per data point was calculated similarly to the edge analysis, except that no gap edges were included in the cover estimates of treated sites (gaps). Observations from both primary plots (100s and 110s), which had more data points, and secondary (replicate) plots (200s and 210s), with less data points, were used to increase the degrees of freedom in the model.

Total biomass in grams/meter$^2$ for each data point was computed using a statistical program which calculated biomass values from the percent vegetation cover data, as well as incorporated data about thick stemmed and weedy species [Means *et al.* 1994, SAS 6.12 (The SAS Institute, 1996)]. Substitutions were made for species without a value in the original equation. All data points in the control and treatment plots (16 total) were included in the biomass analysis and no differentiation was made between gap centers and gap edges. The formula used for biomass were:

Biomass: $b_{jt}$ = biomass per data point (j) of species i, year t

Average biomass per data point of all possible species, year 1*:

$$\overline{B_1} = \frac{\sum_{i=1}^{m} \sum_{j=1}^{n} b_{ij1}}{n}$$

*used a computer formula to actually calculate (SAS)

Average biomass difference (relative change) in cover 1990-1997, per data point of all possible species

$$\text{dif } B_i = \overline{B}_{j2} - \overline{B}_{j1}$$

Absolute change in biomass from 1990 to 1997:

$$\Delta B_i = \frac{\overline{B}_{j2} - \overline{B}_{j1}}{\overline{B}_{j1}}$$

Scatter-plots of biomass and vegetation cover in 1990 and 1997 were created to look for trends between stands. Scatter-plots of percent average cover for most of the target species in 1990 and 1997 were also created (some species had too few data points to be plotted).

Individual species analyses were simply a subset of the vegetation cover analysis. Instead of 12 species combined together, the data for a single species were analyzed. Gap edge data points were not included in this analysis.

A dominance-diversity curve to compare pre- and post- treatment effects and overarching trends was also created and incorporated biomass cover data for all

115 species, including tree seedlings under five cm diameter at breast height (dbh). Dominance refers to the amount of vegetation cover in a plot, while diversity refers to the total number of species found at a plot.

## 2.7 Statistical Analysis

Statistical models were created to test the null hypothesis that there is not a gap effect (i.e., change is not attributable to gap creation [treatment]) for understory vegetation in terms of site, species or edges. A general linear model with a Type III Sum of Squares test was used for each of the models (GLM procedure in SAS 6.12 [SAS Institute Inc. 1996]). Both full and reduced models were tested for all dependent variables. Statistical advice came from Vicente Monleon (Oregon State University, Department of Forest Science, personal communication 1998)

1a) Gap edges were compared to gap centers using the variables "site" and "edge" (gap edge or gap center) to test for "edge effects" after gap creation. Two models were tested. The first model used average cover in 1997 as the response variable, with average cover in 1990 as a covariate. This model tests the question "In 1997 (seven years after gap creation), was understory vegetation cover greater in gaps than at gap edges?" This model was:

$\mu(\text{cover97}) = \beta_0 + \beta_1\ \text{cover90} + \beta_2\ \text{edge} + \beta_3\ \text{site} + \beta_4\ \text{edge*site}$

(Note: It was not necessary to test cover90*edge since no edges existed in 1990.)

1b) The second edge model used the difference between average cover in 1997 from average cover in 1990 as the response variable. This model tested the question "Was the change in percent plant cover the same in the gaps as at the gap edges?" This model also was tested using a percent change variable of: [(cover in 1997- cover in 1990)/ cover in 1990]. The models were:

$$\mu \text{ (relative } \Delta) = \beta_0 + \beta_1 \text{ edge} + \beta_2 \text{ site} + \beta_3 \text{ edge*site}$$

$$\mu \text{ (absolute } \Delta) = \beta_0 + \beta_1 \text{ edge} + \beta_2 \text{ site} + \beta_3 \text{ edge*site}$$

In addition, means were calculated for each site and treatment combination. Since assumptions of normality, independence and an absence of outliers were met for both models, no transformations were needed.

2a) The next tests were to determine the interactive effects of site and gap creation (treatment) on percent cover of understory vegetation and understory biomass. Three models were run using percent average cover and biomass as independent variables. The response variables included: percent average cover or biomass in 1997, the difference in percent average cover or biomass from 1990 to 1997, and the percent change of percent average cover or biomass from 1990 to 1997 (using the equation [(biomass 1997- biomass 1990)/biomass 1990]. In the first model, average cover or biomass in 1997 was the response variable and average cover or biomass in 1990 was a covariate, since it is likely that that cover or biomass in 1997 was influenced by the amount of cover or biomass in 1990. Ignoring cover in 1990 might also hide the effects of treatment and thus become a confounding variable.

The percent average cover models were:

$\mu$ (cover 1997) = $\beta_0 + \beta_1$ cover90 + $\beta_2$ gap + $\beta_3$ site + $\beta_4$ site*gap

$\mu$ (relative $\Delta$ in cover 97-90) = $\beta_0 + \beta_1$ gap + $\beta_2$ site + $\beta_3$ gap*site

$\mu$ (absolute $\Delta$ 1990–1997 ) = $\beta_0 + \beta_1$ gap + $\beta_2$ site + $\beta_3$ gap*site

Change in cover from 1990 to 1997 was the response variable, "gap," indicated a control or a treatment (gap = treatment), and "site" referred to the four stands.

The biomass models were:

$\mu$ (biomass 1997) = $\beta_0 + \beta_1$biomass1990 + $\beta_2$ gap + $\beta_3$ site

$\mu$ (difference in biomass 97-90) = $\beta_0 + \beta_1$gap + $\beta_2$ site

$\mu$ (biomass $\Delta$ 1990-1997) = $\beta_0 + \beta_1$gap + $\beta_2$ site

Change in biomass from 1990 to 1997 was the response variable, "gap," indicated a control or a treatment (gap = treatment), and "site" referred to the four stands.

3) In order to test if species differed by site due to a "gap effect" a model was tested on each of the 12 species. Each species model included 16 observations- one observation for each plot (less when no species were present at a plot). The models also tested how individual species responded after gap creation:

$\mu$( relative $\Delta$ species cover) = $\beta_0 + \beta_1$ gap + $\beta_2$ site + $\beta_3$site*gap

*Rhododendron macrophyllum* was not tested individually since it is only found at the H.J. Andrews and thus had only four observations.

## 2.8 Mapping

Three maps were created for each plot: tree stems and data points, canopy outlines and data points, and contours of biomass abundance. The tree stem and canopy outline maps were created using ArcInfo 7.1 Unix software (ESRI, 1996) and PC ArcView 3.1 software (ESRI, 1996). Sampling locations (data points) were linked to the spatial points within the GIS. Contour maps of biomass abundance were created in Surfer Version 6.01 (Golden Software 1995) using ASCII files containing x, y, and z variables. ArcInfo was used to explore alternate interpolation techniques, such as nearest neighbor, standard and universal kriging, and inverse distance weighting. Inverse distance weighting interpolation was used in the final analysis since it is the most common type of interpolation, it does not alter the z (biomass) value as would other techniques such as kriging, and because the points are not clustered, but evenly spaced (ESRI 1997). The final maps were created in Surfer since the software was easier to manipulate and provided a cleaner map than ArcInfo.

Since plot biomass values spanned a wide range (0.1 to 6000 grams/ $m^2$), biomass values were transformed by the natural logarithm ($\log_e$) for comparative purposes. The natural log scale for all plots ranges from -2 to 8. Only primary plots were mapped (100s and 110s) since secondary plots had too few data points for accurate representation. Maps were created for 1990, 1997 and the difference between 1990 to 1997.

# 3. RESULTS

## 3.1 Edge Importance

In 1990, before treatment, percent cover was significantly greater in edges than gaps at H. J. Andrews and Panther Creek, but it was not significantly different at Martha Creek and Trout Creek (Table 4, Figure 5). Cover in both gap edges and gap centers at H.J. Andrews were the lowest of any of the four stands, while cover was highest at Panther Creek in both gap edges and gap centers.

In 1997, six-growing seasons after gap creation, all gap centers had greater percent cover of understory vegetation than gap edges (Table 4). In 1997, average vegetation cover for gap centers (51%) was 1.5 times greater than the combined vegetation cover for gap edges (33%). However, gap centers responded differently at different sites with Martha Creek having the greatest cover (76%) and H. J. Andrews having the least (27%).

Average vegetation cover in all gap centers increased from 30% in 1990 to 51% in 1997, but stayed constant at 33% in gap edges from 1990 to 1997. (Table 4). Vegetation cover in gap centers increased least at Panther Creek (from 47% in 1990 to 63% in 1997) and most at Martha Creek (from 45% in 1990 to 76% in 1997) (Figure 5). However, relative changes in vegetation cover were greatest at H. J. Andrews where vegetation cover in gap centers increased from 5% in 1990 to 27% in 1997, an increase of nearly 400% (Table 4). Although cover in gap edges did not change significantly at Martha Creek, Trout Creek or Panther Creek

**Table 4:** Means and standard error for percent average cover per data point for gap centers plots and gap edges. Positive values are increases in percent cover, while negative values indicate decreases in cover.

| site | n (# plots) | edge/ gap | mean 1990 (%) | SE | mean 1997 (%) | SE | mean diff (1997-1990) (%) | SE | mean change (%) | SE |
|---|---|---|---|---|---|---|---|---|---|---|
| *edge/gap- all sites* | | | | | | | | | | |
| all | 8 | e | 33 | 7.5 | 33 | 6.3 | 0 | 1.9 | 18 | 15 |
| all | 8 | g | 30 | 6.6 | 51 | 7.4 | 21 | 2.6 | 142 | 55 |
| *edge/gap by combined study sites* | | | | | | | | | | |
| HJA | 2 | e | 10 | 1.1 | 18 | 1.6 | 8 | 0.5 | 86 | 4 |
| HJA | 2 | g | 5 | 0.5 | 27 | 4.9 | 21 | 4.3 | 388 | 43 |
| MCY | 2 | e | 38 | 4.9 | 34 | 7.3 | -3 | 2.4 | -10 | 8 |
| MCY | 2 | g | 45 | 4.8 | 76 | 0.2 | 31 | 4.6 | 70 | 18 |
| PCM | 2 | e | 61 | 8.9 | 58 | 5.8 | -2 | 3.1 | -3 | 5 |
| PCM | 2 | g | 47 | 0.9 | 63 | 4.8 | 16 | 3.9 | 33 | 8 |
| TCO | 2 | e | 23 | 6.0 | 22 | 4.2 | -1 | 1.8 | -3 | 7 |
| TCO | 2 | g | 23 | 4.3 | 40 | 4.0 | 17 | 0.3 | 79 | 16 |
| *edge/gap by study site* | | | | | | | | | | |
| HJA110 | 1 | g | 5 | - | 22 | - | 17 | - | 344 | - |
| HJA210 | 1 | g | 6 | - | 32 | - | 26 | - | 431 | - |
| HJA110 | 1 | e | 9 | - | 16 | - | 8 | - | 91 | - |
| HJA210 | 1 | e | 11 | - | 19 | - | 9 | - | 82 | - |

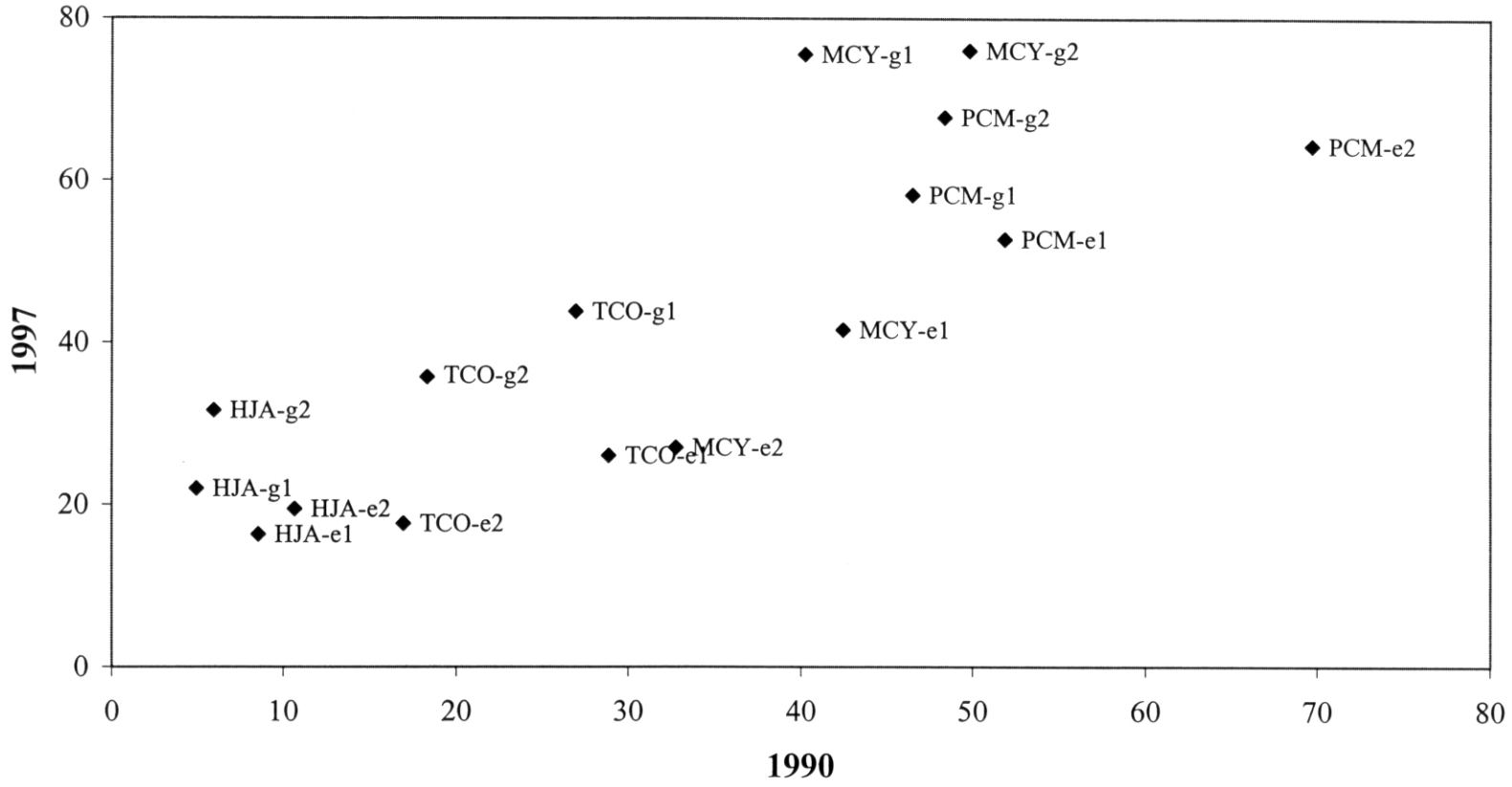
(continued)

**Table 4 (continued)**

*edge/gap by study site*

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| MCY110 | 1 | g | 40 | - | 76 | - | 35 | - | 88 | - |
| MCY210 | 1 | g | 50 | - | 76 | - | 26 | - | 53 | - |
| MCY110 | 1 | e | 42 | - | 42 | - | -1 | - | -2 | - |
| MCY210 | 1 | e | 33 | - | 27 | - | -6 | - | -18 | - |
| | | | | | | | | | | |
| PCM110 | 1 | g | 46 | - | 58 | - | 12 | - | 25 | - |
| PCM210 | 1 | g | 48 | - | 68 | - | 19 | - | 40 | - |
| PCM110 | 1 | e | 52 | - | 53 | - | 1 | - | 2 | - |
| PCM210 | 1 | e | 70 | - | 64 | - | -5 | - | -8 | - |
| | | | | | | | | | | |
| TCO110 | 1 | g | 27 | - | 44 | - | 17 | - | 62 | - |
| TCO210 | 1 | g | 18 | - | 36 | - | 17 | - | 95 | - |
| TCO110 | 1 | e | 29 | - | 26 | - | -3 | - | -10 | - |
| TCO210 | 1 | e | 17 | - | 18 | - | 1 | - | 4 | - |

**Figure 5:** Scatterplot of percent average cover in gap edges and gap centers at treatment sites in 1990 and 1997. Sites above the 45 degree line increased in cover from 1990 to 1997, while values below decreased in cover ('e' =edge, 'g' =gap).



between 1990 and 1997, vegetation in gap edges at H.J. Andrews increased from 10% in 1990 to 18% in 1997, an increase of 86% (Table 4).

Vegetation cover was significantly higher in gap centers in 1997 than 1990 ($r^2 = .98$, $p > 0.0001$) (Table 5). Vegetation cover increased significantly more in gap centers than gap edges from 1990 to 1997 based both on absolute change (model 3, $r^2 = .94$, $p > 0.0003$) as well as relative change (model 4, $r^2 = .98$, $p > 0.0001$). However, both the relationship in vegetation cover between gap edges and gap centers and the amount of change in vegetation cover from 1990 to 1997 differed significantly between sites.

## 3.2 Treatment/Control Importance: Vegetation Cover and Biomass

Percent vegetation cover for the combined control plots changed negligibly from 1990 to 1997, but increased in the treatment plots from 1990 to 1997 (Table 6, Figure 6). Percent vegetation cover in control plots averaged 28% in 1990, and 26% in 1997. Percent vegetation cover in the treatment plots averaged 31% in 1990 and 51% in 1997, an absolute change of 20%.

Initial cover in treatment plots in 1990 was greatest in the two mature sites: Panther Creek (47%), followed by Martha Creek (45%) (Table 6, Figure 6). Treatment plots in the two old-growth sites had less cover than the mature sites in 1990, with 23% at Trout Creek and 8% at H. J. Andrews. Average cover values for

**Table 5:** Results of four General Linear Models for average percent cover of understory vegetation in gap edges and gap centers in 16 plots (two treated, two control, at each of four sites. Factor abbrevations are: GAP = treated site (vs. control), SITE = location, EDGE = plots in edge (0 for edge, 1 for in gap).

| Dependent variable | Independent variable | df | Type III SS | F | P | R-Square |
|---|---|---|---|---|---|---|
| 1 *Edge 1997* | | 8 | 6495.32 | 44.72 | 0.0001 | 0.98 |
| | COVER90 | 1 | 212.14 | 11.68 | 0.0112 | |
| | EDGE | 1 | 1518.55 | 83.63 | 0.0001 | |
| | SITE | 3 | 144.85 | 2.66 | 0.1294 | |
| | EDGE*SITE | 3 | 261.85 | 4.81 | 0.0401 | |
| 2 *Edge 1997 (w/out COVER90)* | | 7 | 6283.18 | 21.17 | 0.0001 | 0.95 |
| | EDGE | 1 | 1326.6 | 32.28 | 0.0005 | |
| | SITE | 3 | 4136.85 | 32.52 | 0.0001 | |
| | EDGE*SITE | 3 | 819.74 | 6.44 | 0.0158 | |
| 3 *Absolute change 1997-1990* | | 7 | 2183.99 | 16.91 | 0.0003 | 0.94 |
| | EDGE | 1 | 1732.02 | 93.86 | 0.0001 | |
| | SITE | 3 | 198.39 | 3.58 | 0.0661 | |
| | EDGE*SITE | 3 | 253.58 | 4.58 | 0.0379 | |
| 4 *Relative Change 1997-1990* | | 7 | 23.79 | 51.16 | 0.0001 | 0.98 |
| | EDGE | 1 | 6.22 | 93.66 | 0.0001 | |
| | SITE | 3 | 13.28 | 66.61 | 0.0001 | |
| | EDGE*SITE | 3 | 4.29 | 21.54 | 0.0003 | |

**Table 6:** Means and standard errors for percent average cover of the combined 12 species of interest from 1990 to 1997. Positive values indicate increases in percent cover, while negative values indicate decreases in cover.

| site | treatment/ control | n (# sites) | n (sps obs) | 1990 mean cov/plot (%) | SE* | 1997 mean cov/plot (%) | SE* | '90-'97 mean cov/plot (%) | SE* |
|---|---|---|---|---|---|---|---|---|---|
| *all sites* | | | | | | | | | |
| all | c | 8 | 96 | 28 | 6.5 | 26 | 5.3 | -3 | 2.1 |
| all | t | 8 | 96 | 31 | 6.3 | 51 | 7.7 | 20 | 2.7 |
| *treatment replicates* | | | | | | | | | |
| HJA | t | 2 | 24 | 8 | 3.2 | 24 | 2.1 | 16 | 1.1 |
| MCY | t | 2 | 24 | 45 | 4.8 | 76 | 0.2 | 31 | 4.6 |
| PCM | t | 2 | 24 | 47 | 0.9 | 63 | 4.8 | 16 | 3.9 |
| TCO | t | 2 | 24 | 23 | 4.3 | 40 | 4.0 | 17 | 0.3 |
| *control replicates* | | | | | | | | | |
| HJA | c | 2 | 24 | 9 | 0.4 | 9 | 1.7 | 1 | 1.3 |
| MCY | c | 2 | 24 | 51 | 2.0 | 40 | 0.5 | -12 | 1.5 |
| PCM | c | 2 | 24 | 39 | 1.1 | 39 | 0.5 | 0 | 0.6 |
| TCO | c | 2 | 24 | 15 | 0.8 | 15 | 4.0 | 0 | 3.2 |
| *treatment-all* | | | | | | | | | |
| HJA110 | t | 1 | 12 | 5 | - | 22 | - | 17 | - |
| HJA210 | t | 1 | 12 | 11 | - | 26 | - | 15 | - |
| MCY110 | t | 1 | 12 | 40 | - | 76 | - | 35 | - |
| MCY210 | t | 1 | 12 | 50 | - | 76 | - | 26 | - |
| PCM110 | t | 1 | 12 | 46 | - | 58 | - | 12 | - |

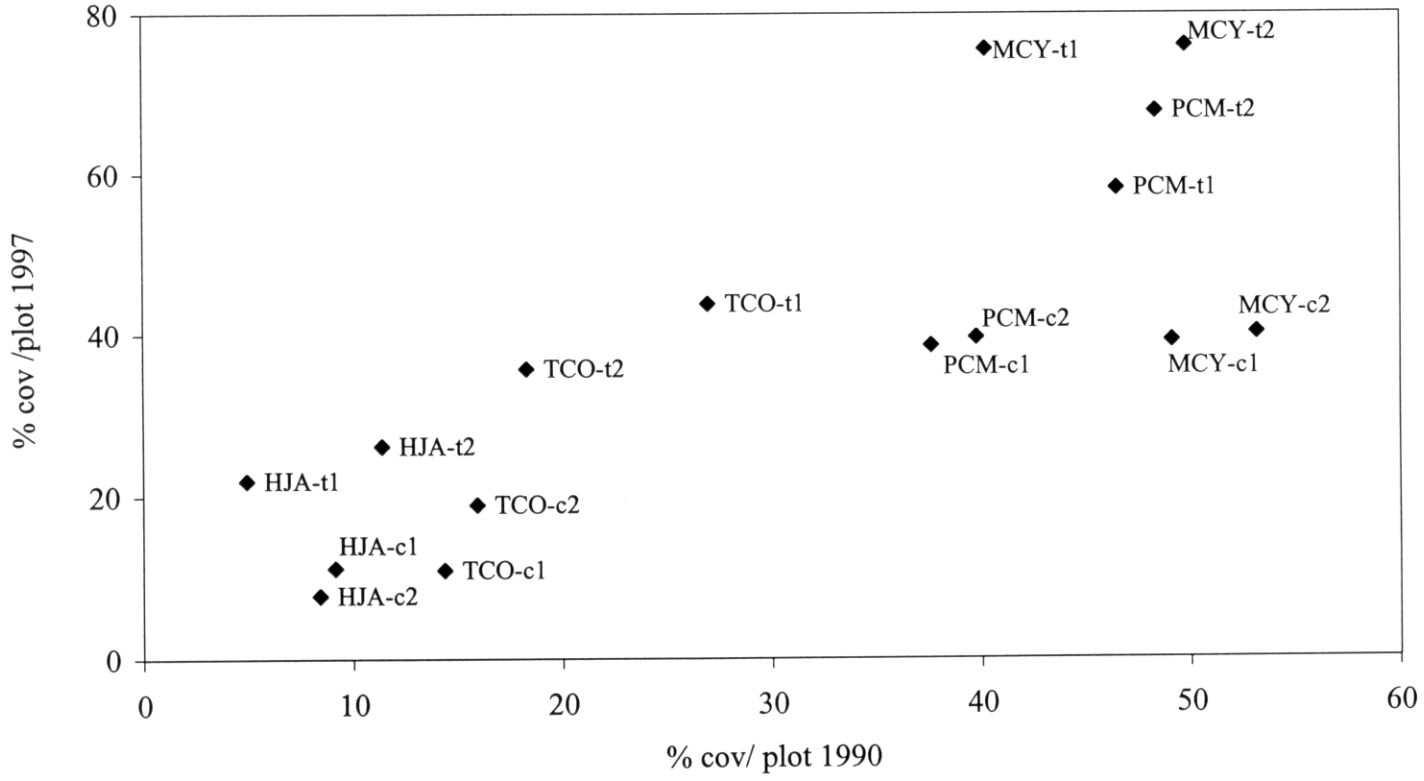
(continued)

**Table 6 (continued)**

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| PCM210 | t | 1 | 12 | 48 | - | 68 | - | 19 | - |
| TCO110 | t | 1 | 12 | 27 | - | 44 | - | 17 | - |
| TCO210 | t | 1 | 12 | 18 | - | 36 | - | 17 | - |
| *control-all* | | | | | | | | | |
| HJA100 | c | 1 | 12 | 9 | - | 11 | - | 2 | - |
| HJA200 | c | 1 | 12 | 8 | - | 8 | - | -1 | - |
| MCY100 | c | 1 | 12 | 49 | - | 39 | - | -10 | - |
| MCY200 | c | 1 | 12 | 53 | - | 40 | - | -13 | - |
| PCM100 | c | 1 | 12 | 38 | - | 39 | - | 1 | - |
| PCM200 | c | 1 | 12 | 40 | - | 40 | - | 0 | - |
| TCO100 | c | 1 | 12 | 14 | - | 11 | - | -3 | - |
| TCO200 | c | 1 | 12 | 16 | - | 19 | - | 3 | - |

* Standard errors for combined treatments and controls only have two degrees of freedom.

**Figure 6:** Scatterplot of percent average cover in controls and treatments in 1990 and 1997. Sites above the 45 degree line increased in cover from 1990 to 1997, while values below decreased in cover ('c' =control, 't' =treatment. '1' = primary, '2' = secondary).



the control plots in 1990 were lead by Martha Creek (51%), followed by Panther Creek (39%), Trout Creek (15%) and H. J. Andrews (9%).

The rankings of the four sites in 1997 were the same for both treatment plots and control plots. Martha Creek lead (76% in treatments, 40% in controls), followed by Panther Creek (63% in treatments, 39% in controls), then Trout Creek (40% in treatments, 15% in controls) and finally H. J. Andrews (24% in treatments, 9 % in controls).

From 1990 to 1997, the absolute change in vegetation cover increased in treated plots from 1.5 to 3 times. Martha Creek, a mature site, was the most dynamic site and increased 31% (1.5 times increase), while treatment plots in the other three sites all increased similarly at approximately 16%, which is a three-fold increase for H. J. Andrews and almost two-fold for Trout Creek. The only site where controls changed significantly from 1990 to 1997 was Martha Creek, which decreased in average vegetation cover by 12%.

In 1990, biomass of understory vegetation was greater in control plots (334.6 grams/meter$^2$) than treatment plots (249 g/m$^2$). By 1997, biomass of understory vegetation was greater in treatment plots (372.8 g/m$^2$) than control plots (354 g/m$^2$) and had increased by 124 g/m$^2$ (91% increase), compared to only 19 g/m$^2$ (10% increase) in the control plots (Table 7, Figure 7).

Biomass in 1990 ranged from 72 g/m$^2$ (at H. J. Andrews) to 502 g/m$^2$ (at Martha Creek); and biomass in 1997 ranged from 113 g/m$^2$ (at H. J. Andrews) to 613 g/m$^2$ (at Martha Creek) (Table 7, Figure 7). Although Martha Creek had the

**Table 7:** Mean biomass per stand in grams/meter$^2$ including all species found at a stand.

| site | treatment/ control | n (# sites) | 1990 mean cov/plot ($g/m^2$) | SE | 1997 mean cov/plot ($g/m^2$) | SE | Absolute change 90-'97 ($g/m^2$) | SE | Relative change '90-'97 (%) | SE |
|---|---|---|---|---|---|---|---|---|---|---|
| *all sites combined* | | | | | | | | | | |
| all | c | 8 | 334.6 | 50.0 | 353.9 | 53.5 | 19.2 | 21.3 | 10.3 | 4.8 |
| all | t | 8 | 249.0 | 26.2 | 372.8 | 48.8 | 123.8 | 29.3 | 90.8 | 33.0 |
| *replicates* | | | | | | | | | | |
| HJA | c | 2 | 89.8 | 18.8 | 113.3 | 19.0 | 23.5 | 0.2 | 27 | 6 |
| HJA | t | 2 | 72.1 | 6.7 | 279.5 | 62.6 | 207.5 | 69.3 | 300 | 124 |
| MCY | c | 2 | 502.2 | 51.9 | 430.5 | 16.3 | -71.7 | 35.6 | -14 | 6 |
| MCY | t | 2 | 430.2 | 16.7 | 613.1 | 10.0 | 182.9 | 6.7 | 43 | 3 |
| PCM | c | 2 | 252.8 | 47.9 | 273.0 | 56.1 | 20.3 | 8.2 | 8 | 2 |
| PCM | t | 2 | 493.7 | 81.3 | 598.6 | 122.7 | 104.9 | 41.3 | 20 | 5 |
| TCO | c | 2 | 203.2 | 7.6 | 224.3 | 1.9 | 21.2 | 9.6 | 11 | 5 |
| TCO | t | 2 | 192.4 | 34.5 | 467.8 | 53.3 | 275.3 | 18.9 | 146 | 16 |
| *all sites* | | | | | | | | | | |
| HJA100 | c | 1 | 108.7 | - | 132.4 | - | 23.7 | - | 22 | - |
| HJA200 | c | 1 | 71.0 | - | 94.3 | - | 23.3 | - | 33 | - |
| HJA110 | t | 1 | 78.8 | - | 217.0 | - | 138.2 | - | 175 | - |
| HJA210 | t | 1 | 65.3 | - | 342.1 | - | 276.8 | - | 424 | - |

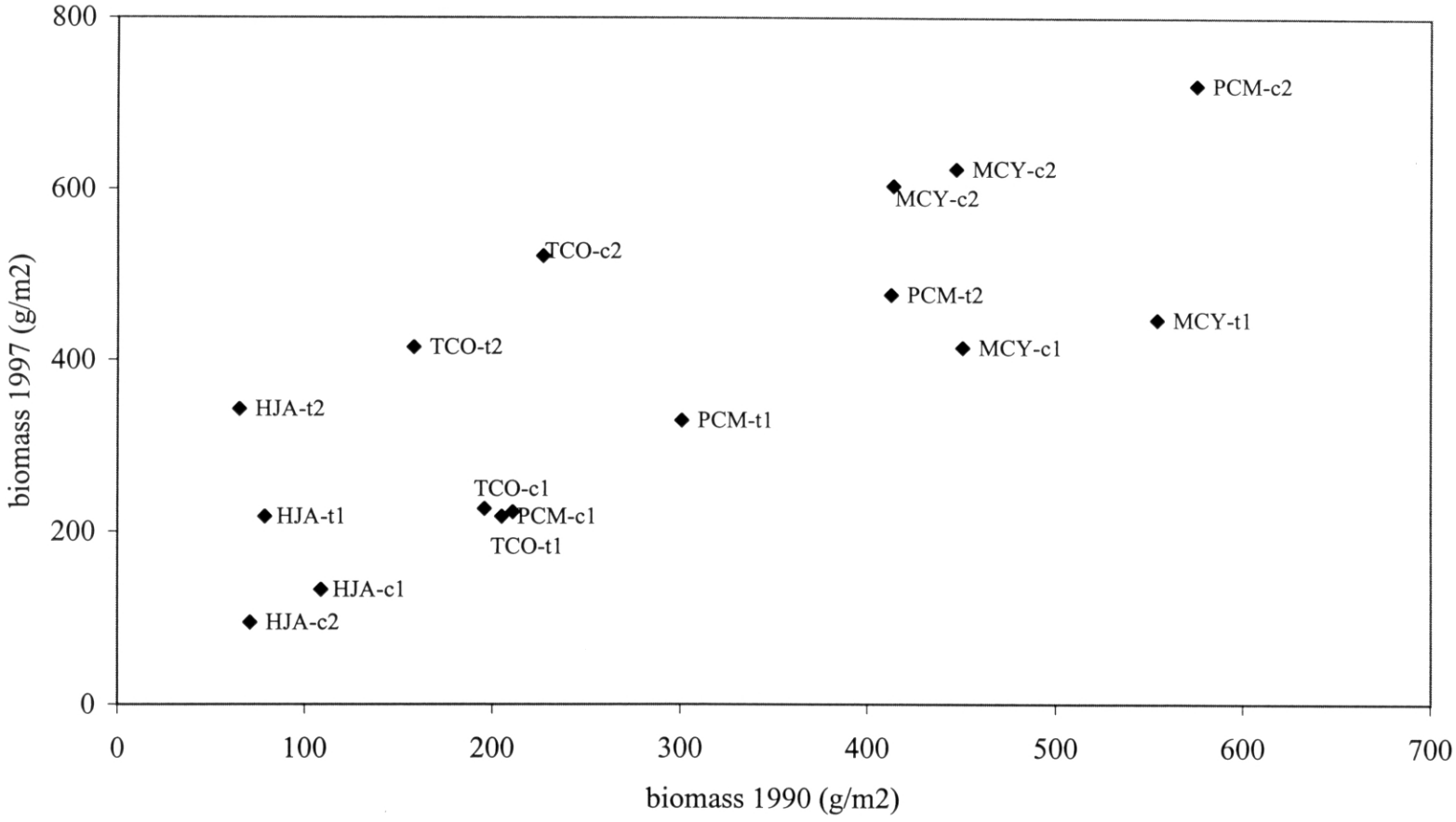
(continued)

**Table 7 (continued)**

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| MCY100 | c | 1 | 450.4 | - | 414.3 | - | -36.1 | - | -8 | - |
| MCY200 | c | 1 | 554.1 | - | 446.8 | - | -107.4 | - | -19 | - |
| MCY110 | t | 1 | 413.5 | - | 603.2 | - | 189.7 | - | 46 | - |
| MCY210 | t | 1 | 446.9 | - | 623.1 | - | 176.2 | - | 39 | - |
| | | | | | | | | | | |
| PCM100 | c | 1 | 204.9 | - | 217.0 | - | 12.0 | - | 6 | - |
| PCM200 | c | 1 | 300.6 | - | 329.1 | - | 28.5 | - | 9 | - |
| PCM110 | t | 1 | 575.0 | - | 721.3 | - | 146.3 | - | 25 | - |
| PCM210 | t | 1 | 412.4 | - | 476.0 | - | 63.6 | - | 15 | - |
| | | | | | | | | | | |
| TCO100 | c | 1 | 195.6 | - | 226.3 | - | 30.7 | - | 16 | - |
| TCO200 | c | 1 | 210.8 | - | 222.4 | - | 11.6 | - | 6 | - |
| TCO110 | t | 1 | 226.9 | - | 521.1 | - | 294.2 | - | 130 | - |
| TCO210 | t | 1 | 158.0 | - | 414.4 | - | 256.5 | - | 162 | - |

* Only two observations per stand, so standard errors not as useful.

**Figure 7:** Scatterplot of biomass in controls and treatments in 1990 and 1997. Sites above the 45 degree line increased in cover from 1990 to 1997, while values below decreased in cover ('c' =control, 't' =treatment. '1' = primary, '2' = secondary).



most biomass of all the control plots in 1990 and all plots in 1997, biomass in 1997 at Martha Creek actually dropped 72 $g/m^2$ (14% decrease) in the control plots, but rose 182 $g/m^2$ (43%) in the gaps. In 1990, Panther Creek gap plots had the most biomass at 494 $g/ m^2$, but ranked second to Martha Creek (599 $g/m^2$ compared to 613 $g/m^2$). Panther Creek was the gap with the least amount of change at 20%, whereas Panther Creek increased 43%, Trout Creek 146% and H. J. Andrews 300%. . H.J. Andrews had the least amount of biomass in 1990 and 1997 compared to the other sites for both gaps and controls.

Vegetation cover was significantly higher in treatment plots in 1997 than 1990 ($r^2 = .99$, $p > 0.0001$) (Table 8). Vegetation cover increased significantly more in treatment plots than control plots from 1990 to 1997 based both on absolute change (model 2, $r^2 = .96$, $p > 0.0001$) as well as relative change (model 3, $r^2 = .80$, $p > 0.0007$). However, both the relationship in vegetation cover between control plots and treatment plots and the absolute change in vegetation cover from 1990 to 1997 differed significantly between sites. Therefore, the amount of vegetation cover will be a function of both treatment and site.

Understory biomass was also significantly higher in treatment plots in 1997 than 1990 ($r^2 = .95$, $p > 0.0001$) (Table 9). Understory biomass increased significantly more in treatment plots than control plots from 1990 to 1997 based both on absolute change (model 2, $r^2 = .83$, $p > 0.0003$) as well as relative change (model 3, $r^2 = .97$, $p > 0.0001$). However, only the relative change in biomass from 1990 to 1997 differed significantly between sites.

**Table 8:** Results of General Linear Model for percent average cover of understory vegetation in all 16 plots (two treatemnt, two control at each of four sites). The three dependent variables are: cover in 1997, the absolute change from 1990-1997, and the relative change from 1990 to 1997. The three independent variables are: GAP = treated site (vs. control), SITE =study site location, COV90 = Percent Cover in 1990. If no interaction affects are shown, they were not significant and were dropped from the model.

| Dependent variable | Independent variable | df | Type III SS | F | P | R-Square |
|---|---|---|---|---|---|---|
| 1 *Percent cover 1997* | | 8 | 7247.12 | 74.50 | 0.0001 | 0.99 |
| | COV90 | 1 | 42.13 | 3.46 | 0.1050 | |
| | GAP | 1 | 1851.57 | 152.28 | 0.0001 | |
| | SITE | 3 | 25.33 | 0.69 | 0.5842 | |
| | GAP*SITE | 3 | 276.19 | 7.57 | 0.0133 | |
| 2 *Absolute Change 1997-1990* | | 7 | 2560.80 | 28.13 | 0.0001 | 0.96 |
| | GAP | 1 | 2028.60 | 155.98 | 0.0001 | |
| | SITE | 3 | 6.62 | 0.17 | 0.9139 | |
| | GAP*SITE | 3 | 525.58 | 13.47 | 0.0017 | |
| 3 *Relative Change 1997-1990* | | 4 | 1.27 | 11.10 | 0.0007 | 0.80 |
| | GAP | 1 | 1.07 | 37.48 | 0.0001 | |
| | SITE | 3 | 0.20 | 2.30 | 0.1336 | |

**Table 9:** Results of General Linear Model for biomass of understory vegetation in all 16 plots (two treatemnt, dependent variables: cover in 1997, the absolute change from 1990-1997, and the relative change from 1990 to 1997. two control at each of four sites). The three dependent variables are: GAP = treated site (vs. control), SITE =study site location, BIO90 = Biomass in 1990. If no interaction affects are shown, they were not significant and were dropped from the model.

| Dependent Variable | Independent Variable | df | Type III SS | F | P | R-Square |
|---|---|---|---|---|---|---|
| 1 *Biomass in 1997* | | 5 | 482245.91 | 35.36 | 0.0001 | 0.95 |
| | BIO90 | 1 | 39718.02 | 14.56 | 0.0034 | |
| | GAP | 1 | 159884.52 | 58.62 | 0.0001 | |
| | SITE | 3 | 8478.63 | 1.04 | 0.4180 | |
| 2 *Absolute change in Biomass (1997-1990 )* | | 4 | 174528.72 | 13.32 | 0.0003 | 0.83 |
| | GAP | 1 | 151101.29 | 46.13 | 0.0001 | |
| | SITE | 3 | 23427.42 | 2.38 | 0.1249 | |
| 3 *Relative Change in Biomass (1997-1990)* | | 7 | 1.16 | 35.57 | 0.0001 | 0.97 |
| | GAP | 1 | 0.61 | 132.11 | 0.0001 | |
| | SITE | 3 | 0.42 | 30.56 | 0.0001 | |
| | GAP*SITE | 3 | 0.12 | 8.39 | 0.0075 | |

## 3.3 Within Plot Patterns

In 1990, patchiness was greatest at the two old-growth stands: H. J. Andrews followed by Trout Creek (Figures 8a and 9a). The two mature stands, Martha Creek and Panther Creek were similar to each other and less patchy (Figures 10a and 11a). In 1997, six growing seasons after treatment, H. J. Andrews and Trout Creek were similarly patchy (Figures 8b and 9b) and both sites were patchier than the two mature sites in 1997 (Figures 10b and 11b). Maps of change from 1990 to 1997 also indicate that the two old-growth sites are similarly patchy and patchier than the two mature stands (Figures 8c-10c). The variability of biomass values between sites was greater in 1990 than 1997.

The primary gap and control at Martha Creek were the only places where decreases in biomass occurred in 1997. After examining the raw data, *Berberis nervosa* was the main species to decrease after gap creation and it occurred mostly along the edges of the primary gap at Martha Creek.

## 3.4 Species' Importance

The combined plot averages for percent cover of most understory species did not change significantly in the controls plots, except for slight decreases in *Berberis nervosa* (2.3% decrease) and *Gaultheria shallon* (1.8 % decrease) (Table

Figure8a: Contour map of the natural logged values of understory vegetation biomass in 1990 at H.J. Andrews, an old-growth site. Dark areas indicate high biomass, while light areas indicate low biomass.

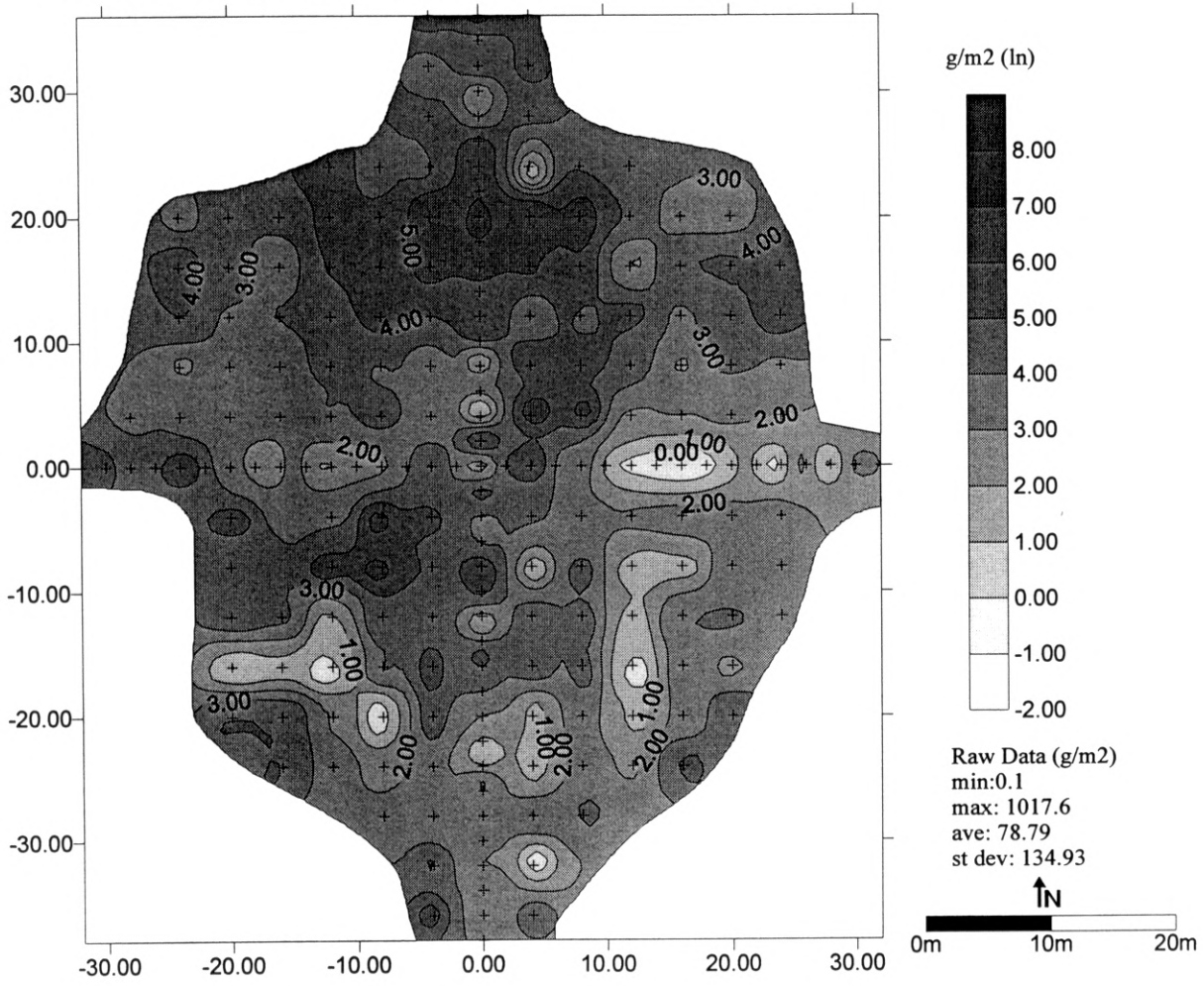


Figure 8b: Contour map of the natural logged values of understory vegetation biomass in 1997 at H.J. Andrews, an old-growth site. Dark areas indicate high biomass, while light areas indicate low biomass.

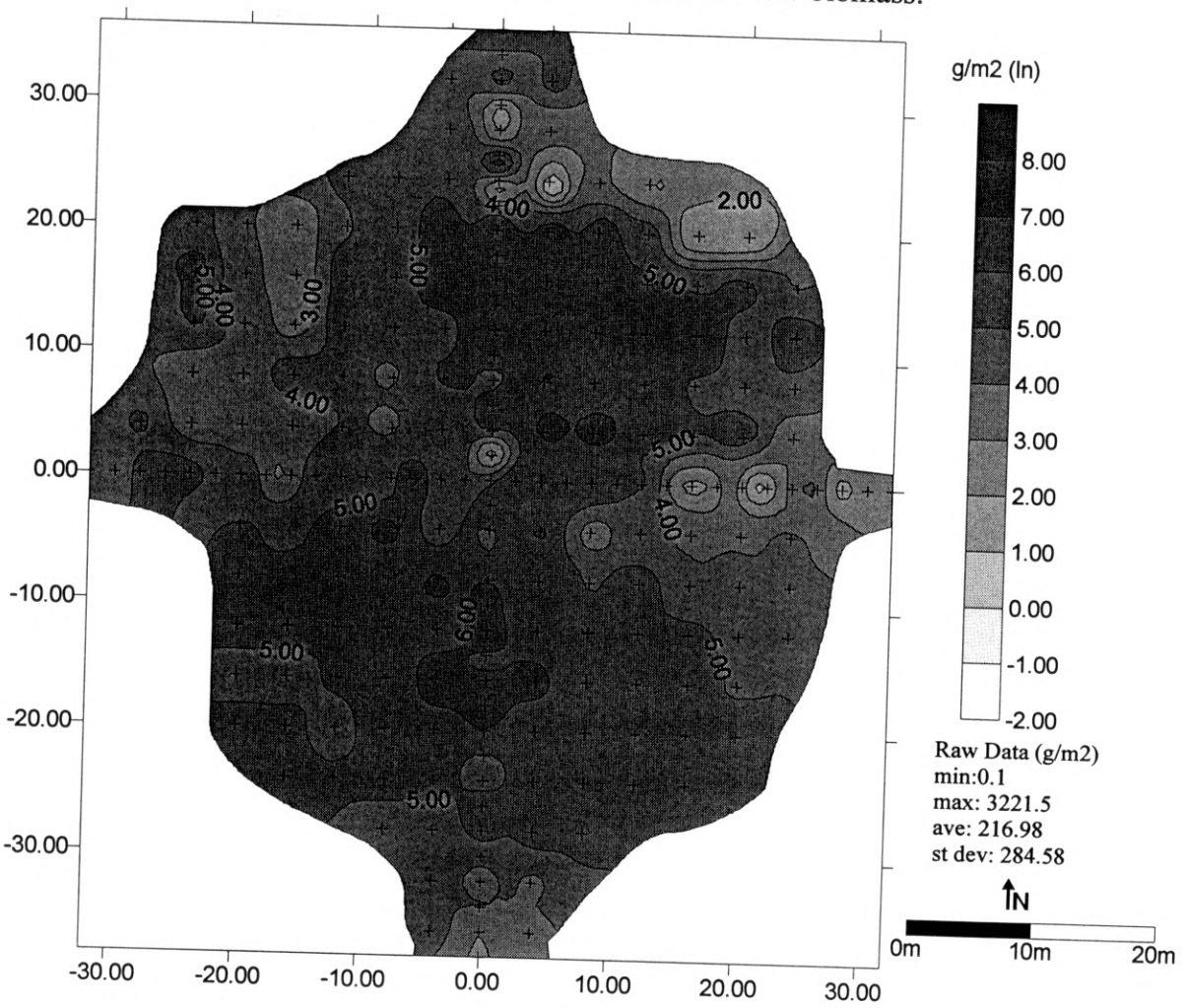


Figure 8c: Contour map of the natural logged difference in understory vegetation biomass from 1990 to 1997 at H.J. Andrews, an old-growth site. Dark areas indicate greater biomass in 1997. Light areas indicate greater biomass in 1990.

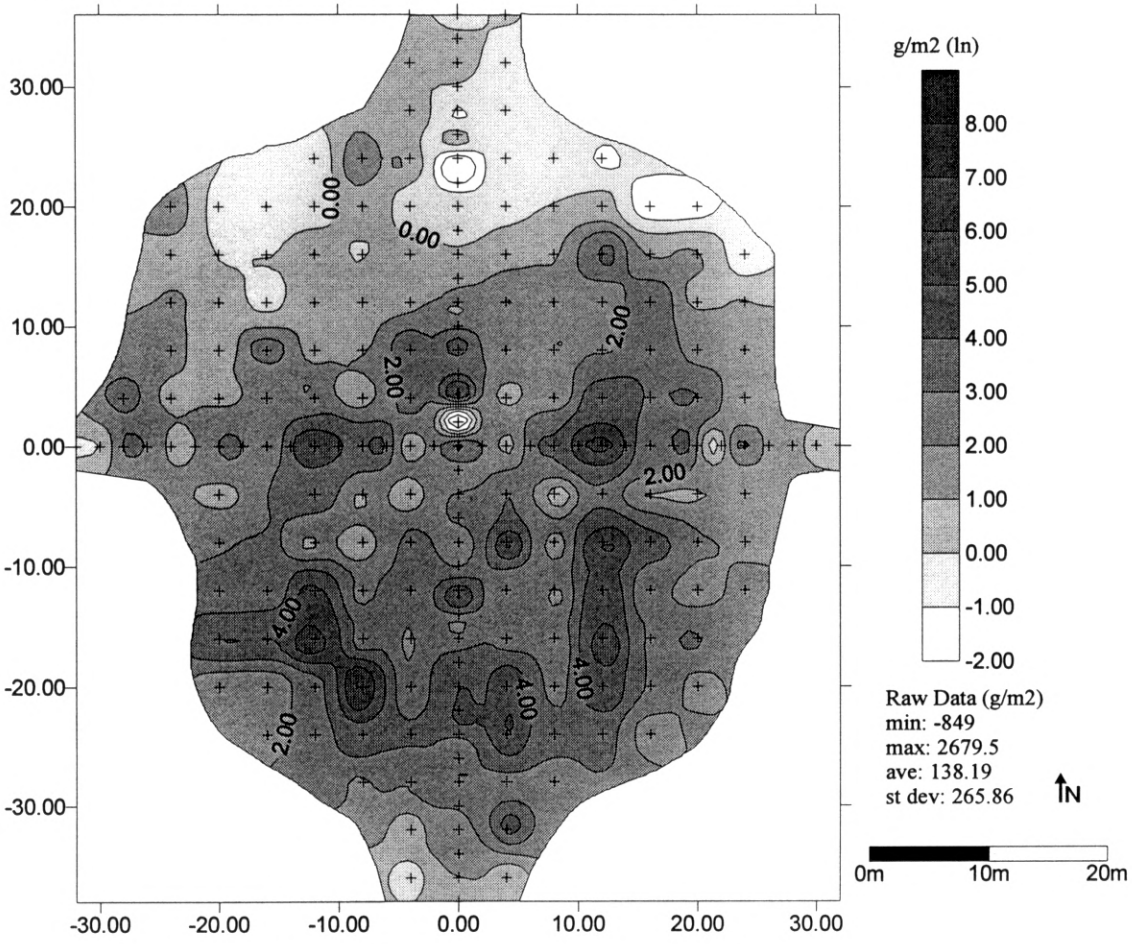


Figure 9a: Contour map of the natural logged values of understory vegetation biomass in 1990 at Trout Creek, an old-growth site. Dark areas indicate high biomass, while light areas indicate low biomass.

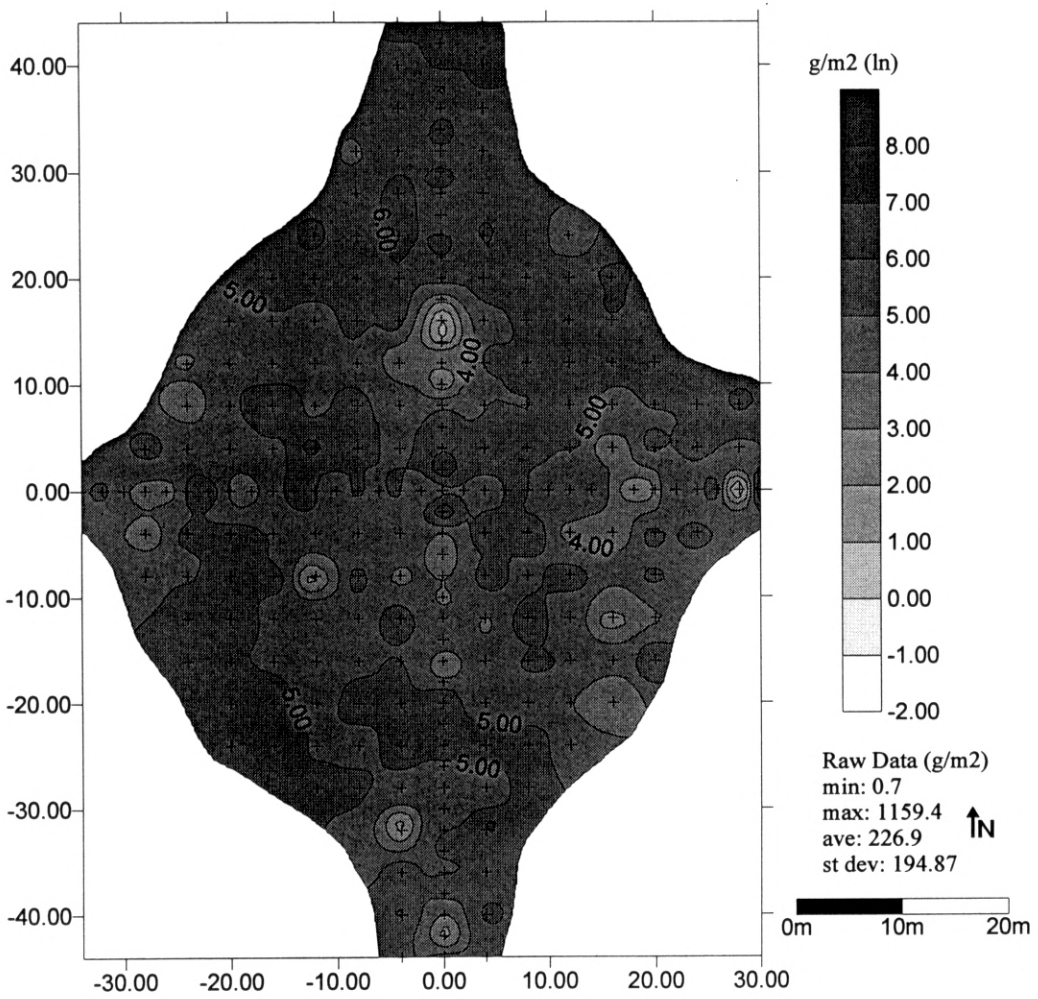


Figure 9b: Contour map of the natural logged values of understory vegetation biomass in 1997 at Trout Creek, an old-growth site. Dark areas indicate high biomass, while light areas indicate low biomass.

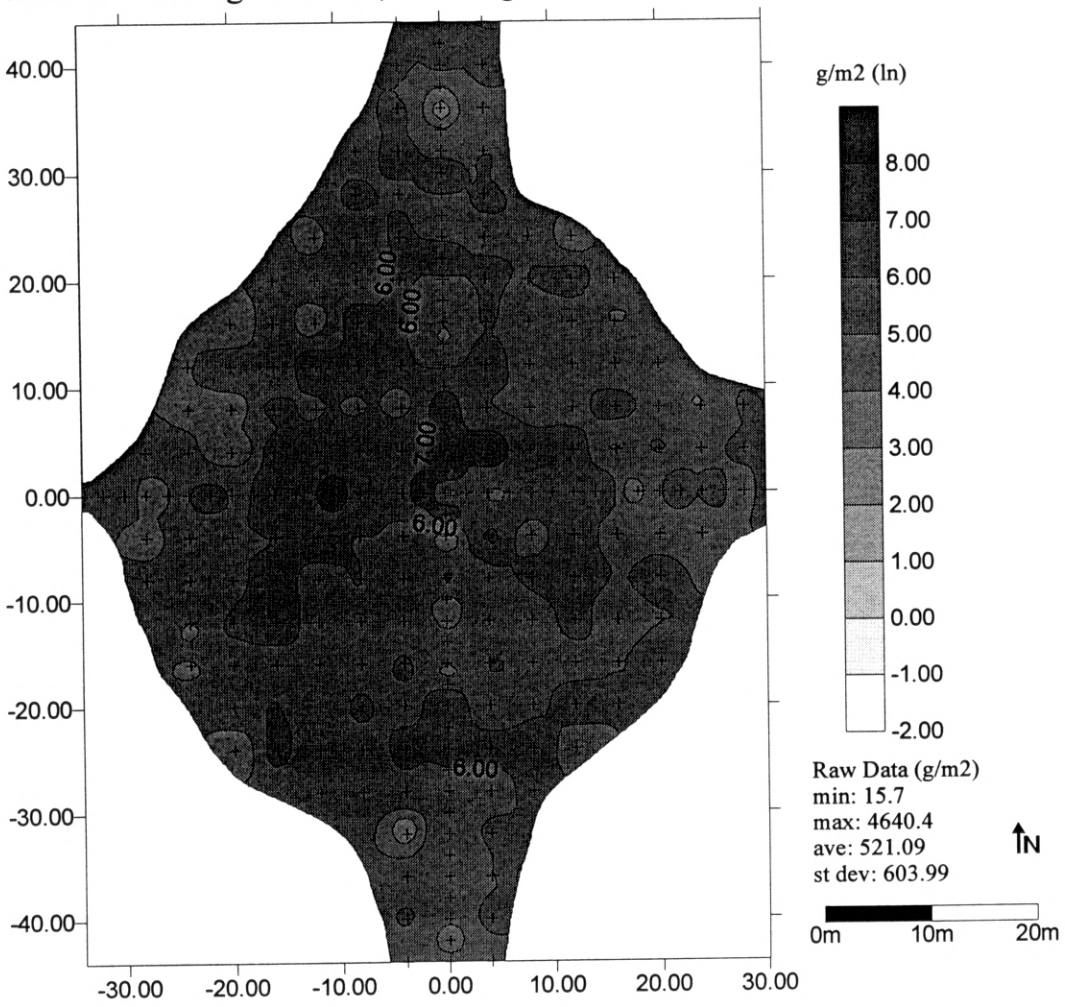


Figure 9c: Contour map of the natural logged difference in understory vegetation biomass from 1990 to 1997 at Trout Creek, an old-growth site. Dark areas indicate greater biomass in 1997. Light areas indicate greater biomass in 1990.

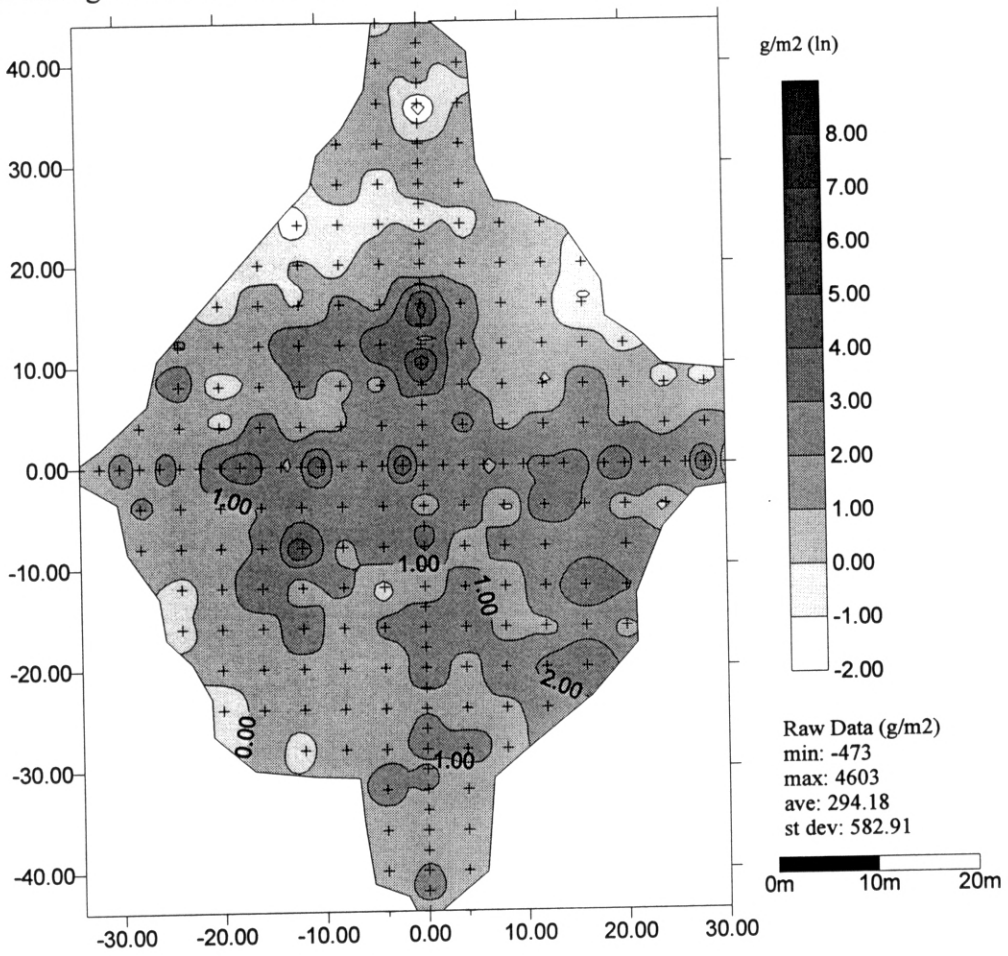


Figure 10a: Contour map of the natural logged values of understory vegetation biomass in 1990 at Martha Creek, a mature site. Dark areas indicate high biomass, while light areas indicate low biomass.

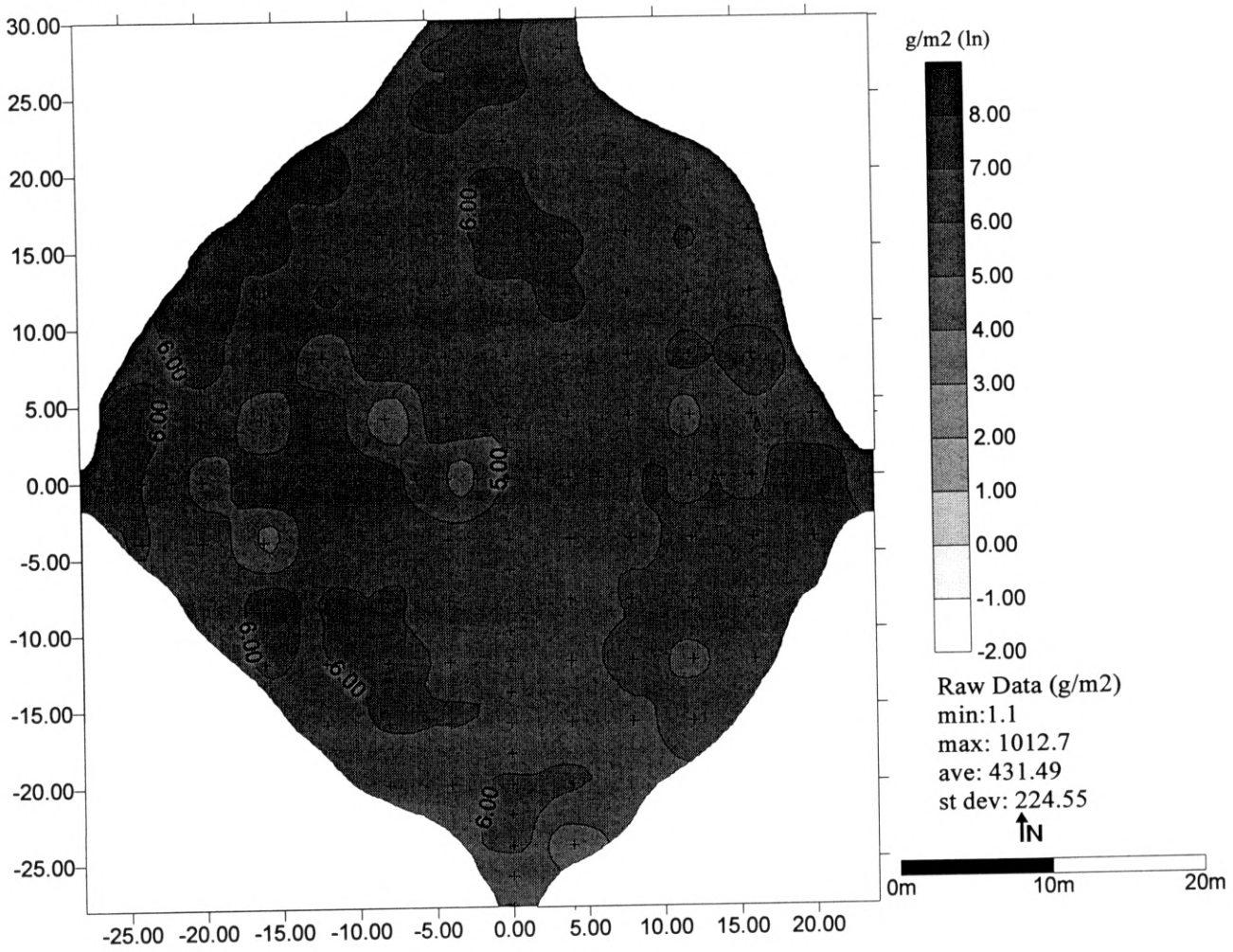


Figure 10b: Contour map of the natural logged values of understory vegetation biomass in 1997 at Martha Creek, a mature site. Dark areas indicate high biomass, while light areas indicate low biomass.

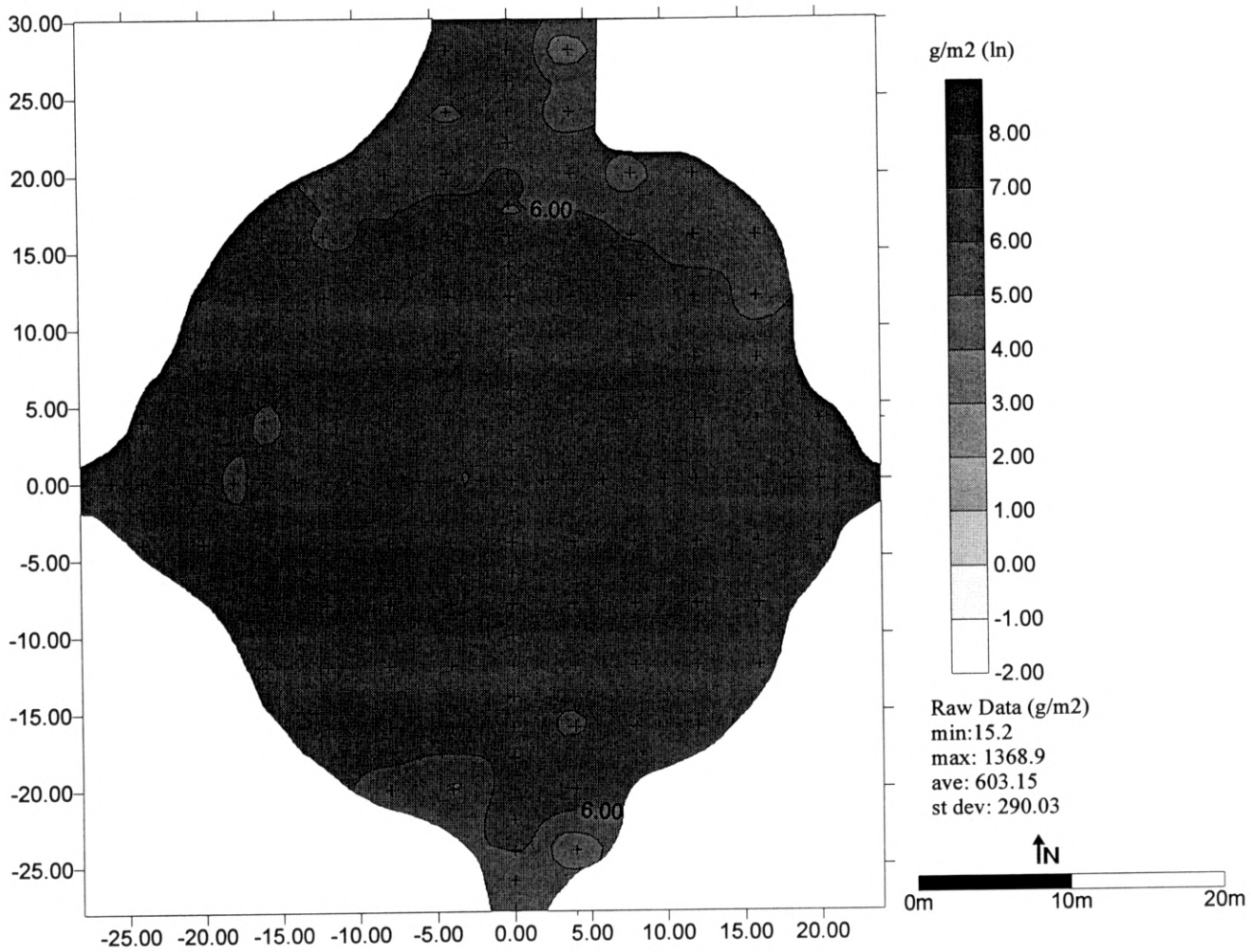


Figure 10c: Contour map of the natural logged difference in understory vegetation biomass from 1990 to 1997 at Martha Creek, a mature site. Dark areas indicate greater biomass in 1997. Light areas indicate greater biomass in 1990.

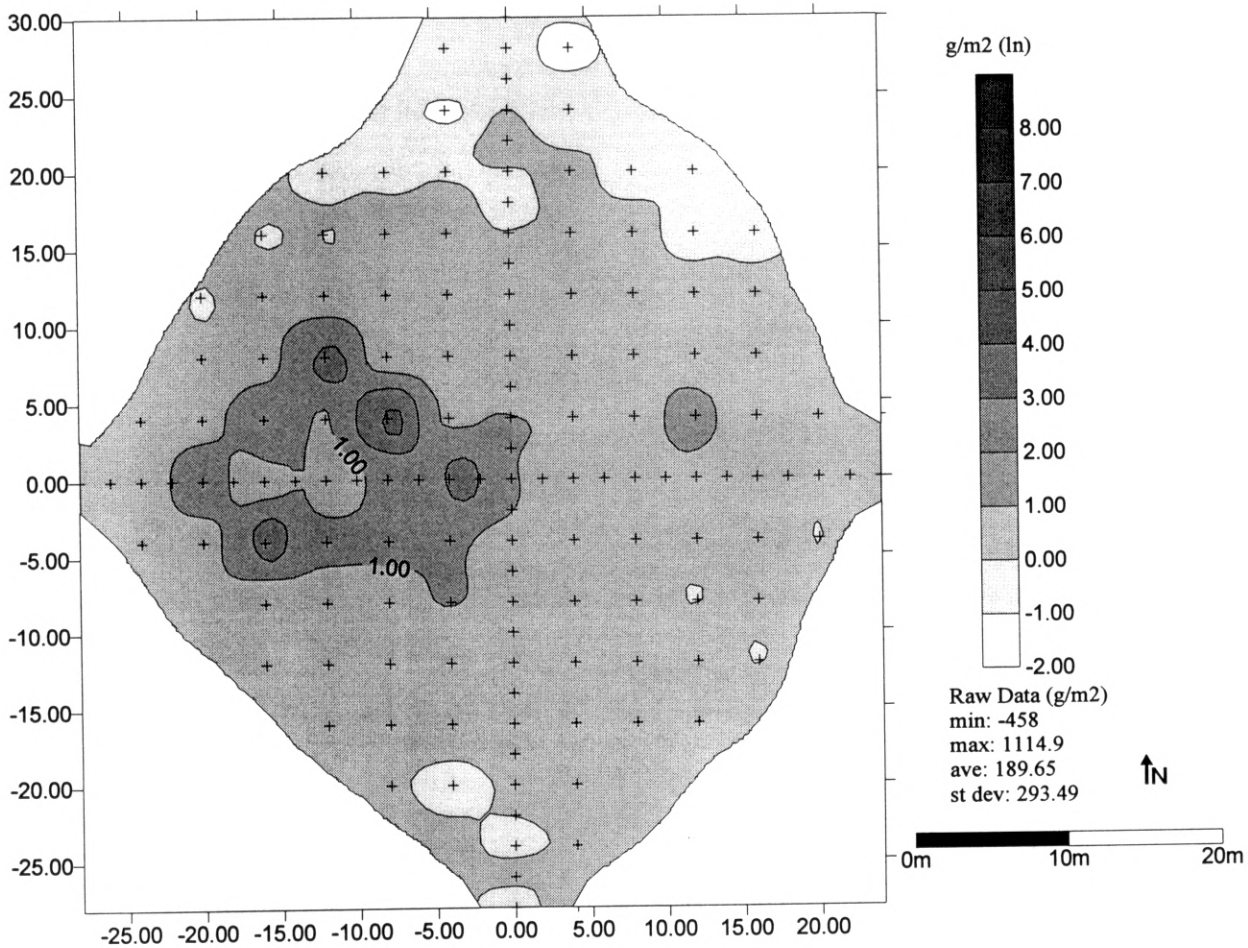


Figure 11a: Contour map of the natural logged values of understory vegetation biomass in 1990 at Panther Creek, a mature site. Dark areas indicate high biomass, while light areas indicate low biomass.

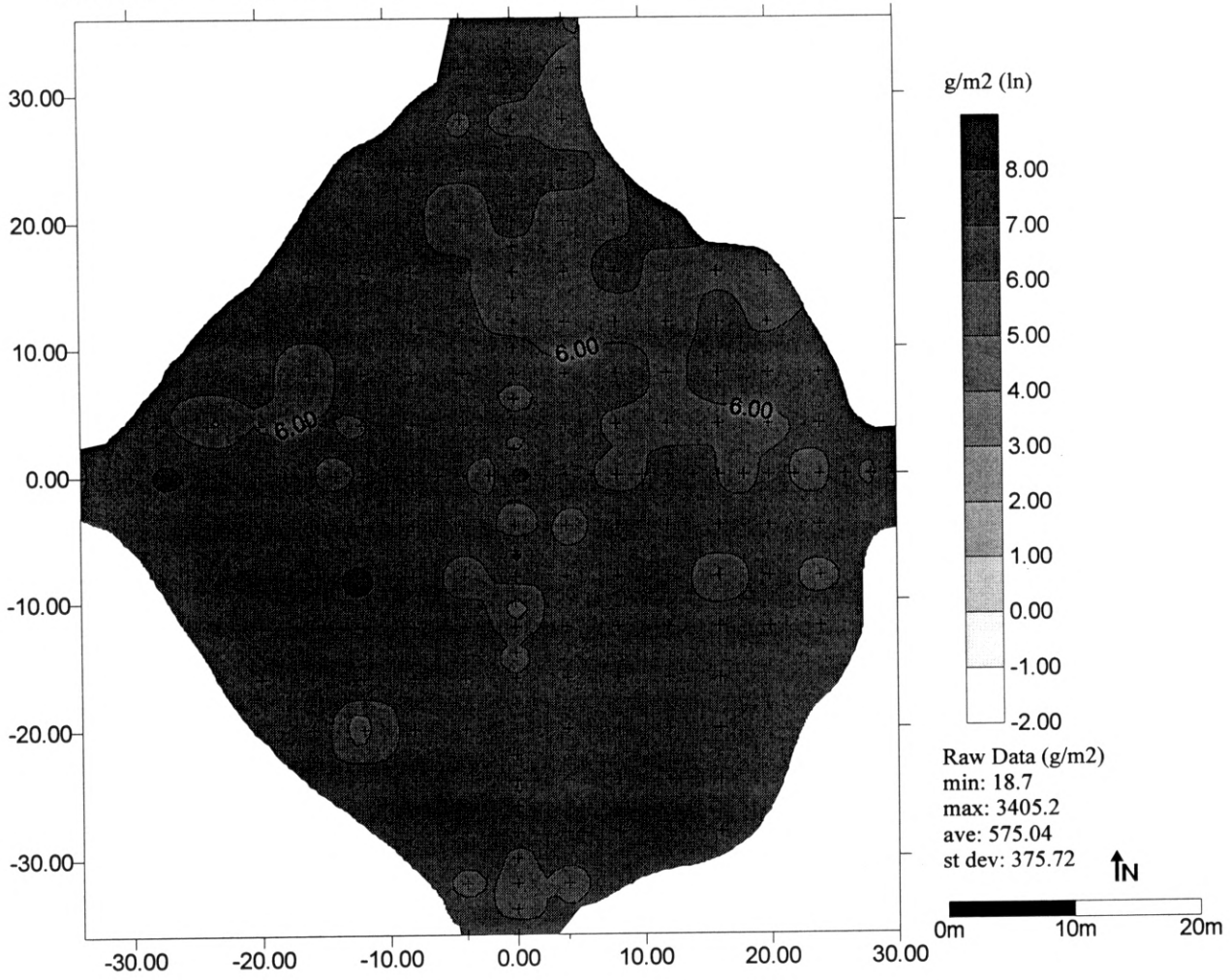


Figure 11b: Contour map of the natural logged values of understory vegetation biomass in 1997 at Panther Creek, a mature site. Dark areas indicate high biomass, while light areas indicate low biomass.

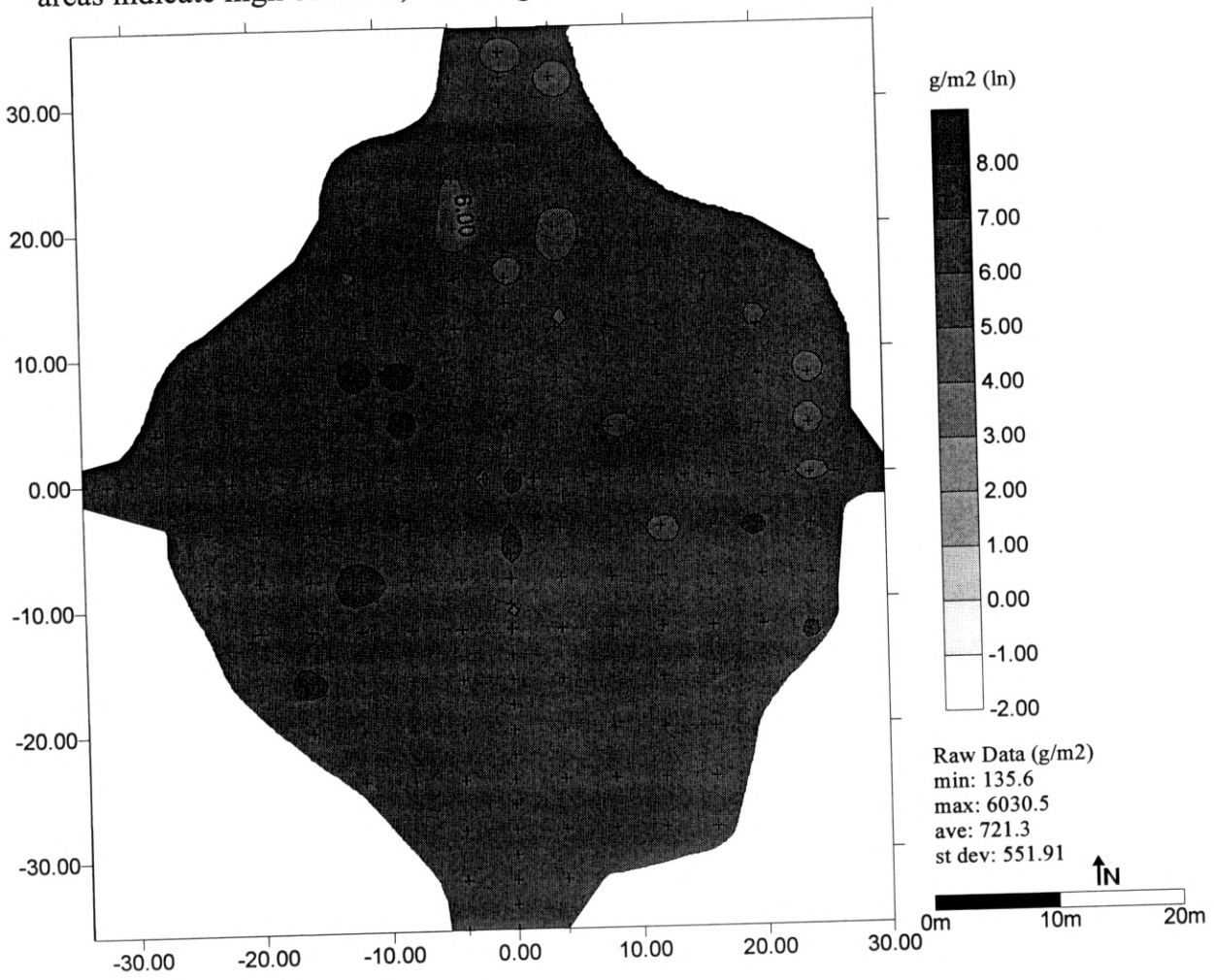
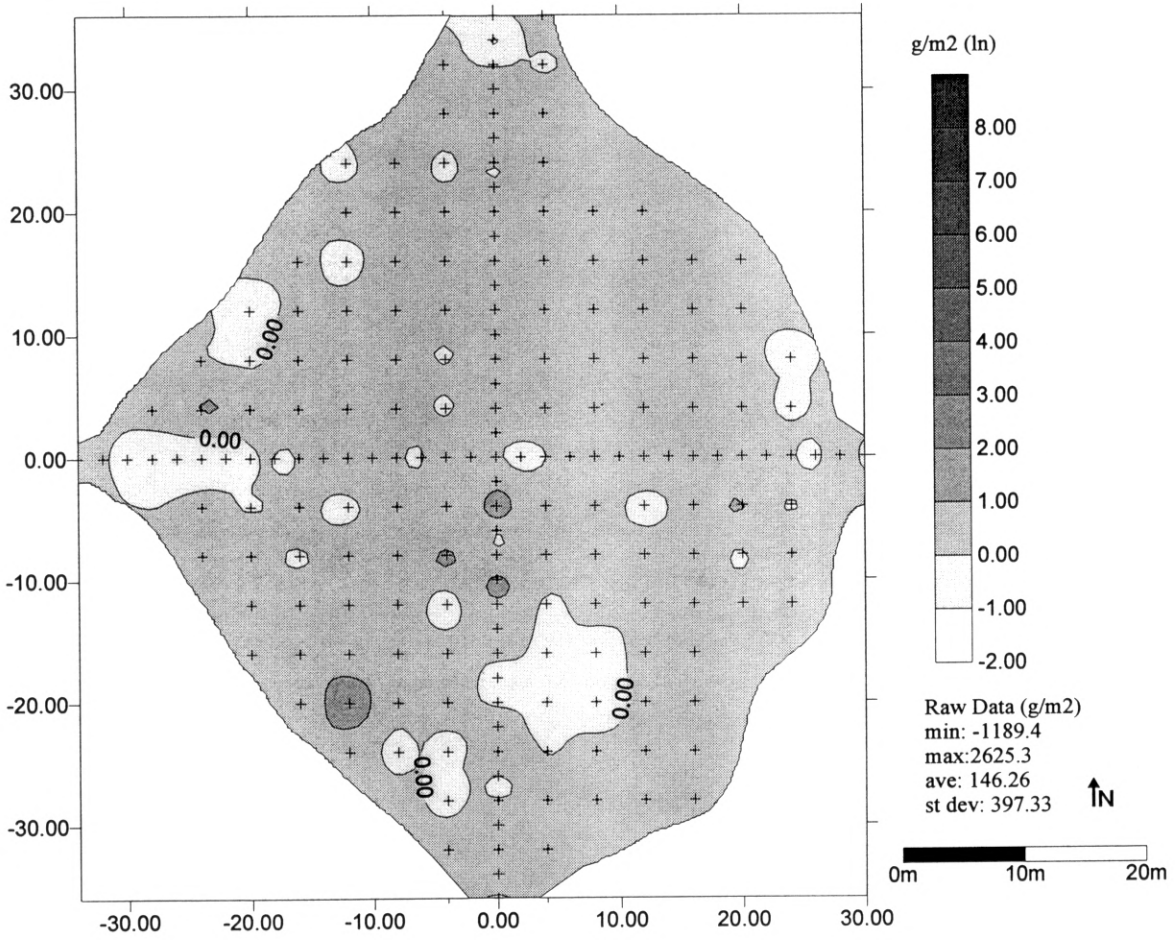


Figure 11c: Contour map of the natural logged difference in understory vegetation biomass from 1990 to 1997 at Panther Creek, a mature site. Dark areas indicate greater biomass in 1997. Light areas indicate greater biomass in 1990.



10). The combined plot averages for treatment plots mostly increased, but treatment plot responses were much more variable than control responses between species. The species with the greatest increases in percent average cover were *Rubus ursinus* (4.9% increase), *Acer cinncinatum* (3.49% increase), *Gaultheria shallon* (3.3% increase), and *Cornus canadensis* (2.9% increase).

*Rubus ursinus* had the most consistent positive responses in the treatment plots (3% to 7% increases) (Figure 12). Three of the 12 target species declined in percent average cover values inside gaps: *Berberis nervosa* (Figure 13) (decreased by 5.8% at Martha Creek), *Vaccinium parvifolium* (Figure 14) (decreased by 1.8% at Trout Creek) and *Rhododendron macrophyllum* (decreased 2.7% at H. J. Andrews, the only place it was found). Average percent cover abundance in gaps for *Gaultheria shallon* (Figure 15) and *Cornus canadensis* (Figure 16) were the most variable. *Gaultheria shallon* increased by 12% at Martha Creek, but remained mostly unchanged at Trout Creek and Panther Creek (it is not found at H. J. Andrews). *Cornus canadensis,* an herb, increased by 11% at Trout Creek, but remained unchanged H. J. Andrews and Panther Creek (and was not found at Martha Creek). *Acer cinncinatum* increased abundance in the treatment plots of the two mature sites, but did not change greatly in the treatment plots of the two old-growth sites (Figure 17).

Both weedy species, *Lactuca muralis* and *Epilobium angustifolium,* invaded in the treatment plots at H.J. Andrews while only *Lactuca muralis* invaded at Martha Creek and Panther Creek and neither species invaded at Trout Creek (Table

**Table 10:** Percent average cover of each species per data point for individual years and combined years. "Total spp" lists how many of the 12 species are found at each plot. Dashes (-) indicate no species present.

| SITES | SPECIES: ACCI | ACTR | BENE | COCA | EPAN | GASH | LAMU | LIBO2 | RHMA | ROGY | RUUR | VAPA | total spp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *all combined (1997-1990)* | | | | | | | | | | | | | |
| control | 0.30 | 1.30 | -2.25 | 0.14 | - | -1.80 | 0.01 | 0.05 | 0.18 | -0.18 | -0.01 | -0.43 | 11 |
| treatment | 3.49 | 1.79 | -0.04 | 2.92 | 1.23 | 3.32 | 1.35 | 1.30 | -0.68 | 0.54 | 4.87 | -0.25 | 12 |
| *controls (1997-1990)* | | | | | | | | | | | | | |
| HJA | 0.50 | 0.00 | -0.69 | 0.21 | - | - | - | 0.19 | 0.71 | - | -0.01 | -0.25 | 7 |
| MCY | 0.87 | -0.02 | -5.37 | - | - | -6.61 | 0.01 | - | - | -0.12 | -0.03 | -0.24 | 8 |
| PCM | -0.21 | 3.45 | -2.54 | -0.08 | - | 0.30 | 0.03 | -0.01 | - | -0.52 | -0.01 | -0.04 | 10 |
| TCO | 0.04 | 1.76 | -0.39 | 0.45 | - | -0.90 | - | 0.03 | - | -0.09 | 0.00 | -1.18 | 4 |
| *treatments (1997-1990)* | | | | | | | | | | | | | |
| HJA | -0.05 | 0.09 | 1.98 | 0.29 | 4.81 | - | 1.30 | 3.09 | -2.72 | 0.14 | 5.93 | 1.01 | 11 |
| MCY | 7.21 | 0.00 | 2.20 | - | 0.02 | 12.34 | 1.39 | - | - | 0.68 | 7.12 | -0.17 | 8 |
| PCM | 7.13 | 6.09 | -5.82 | -0.01 | 0.10 | -0.05 | 2.69 | 0.63 | - | 1.20 | 3.63 | -0.05 | 11 |
| TCO | -0.31 | 0.97 | 1.48 | 11.38 | - | 0.99 | 0.00 | 1.46 | - | 0.13 | 2.80 | -1.79 | 9 |
| *all sites- 1997-1990* | | | | | | | | | | | | | |
| HJA100 | 0.78 | 0.01 | 0.22 | 0.51 | - | - | - | 0.38 | 0.03 | - | 0.13 | -0.05 | 8 |
| HJA110 | -0.07 | 0.18 | 2.51 | 0.20 | 4.04 | - | 0.49 | 1.55 | - | 0.28 | 7.15 | 0.66 | 10 |
| HJA200 | 0.22 | - | -1.60 | -0.09 | - | - | - | 0.00 | 1.40 | - | -0.14 | -0.45 | 6 |
| HJA210 | -0.03 | - | 1.46 | 0.37 | 5.57 | - | 2.11 | 4.64 | -5.44 | - | 4.71 | 1.37 | 9 |

(continued)

**Table 10 (continued)**

| SITES | ACCI | ACTR | BENE | COCA | EPAN | GASH | LAMU | LIBO2 | RHMA | ROGY | RUUR | VAPA | total spp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MCY 100 | 0.41 | -0.07 | -10.34 | - | - | 0.01 | 0.02 | - | - | 0.02 | 0.01 | -0.06 | 8 |
| MCY110 | 7.81 | 0.00 | 3.57 | - | 0.05 | 14.24 | 2.49 | - | - | 0.08 | 7.34 | -0.23 | 8 |
| MCY200 | 1.33 | 0.02 | -0.40 | - | - | -13.22 | - | - | - | -0.26 | -0.07 | -0.42 | 7 |
| MCY210 | 6.62 | 0.00 | 0.83 | - | 0.00 | 10.44 | 0.30 | - | - | 1.27 | 6.89 | -0.10 | 7 |
| PCM100 | -0.25 | 3.92 | -1.95 | - | - | 0.11 | 0.02 | -0.01 | - | -0.76 | -0.08 | -0.08 | 9 |
| PCM110 | 3.34 | 6.02 | -2.54 | -0.02 | 0.12 | -1.01 | 1.06 | 1.26 | - | 0.56 | 3.57 | -0.70 | 11 |
| PCM200 | -0.18 | 2.97 | -3.13 | -0.17 | - | 0.49 | 0.03 | - | - | -0.29 | 0.07 | 0.00 | 8 |
| PCM210 | 10.91 | 6.16 | -9.09 | - | 0.09 | 0.91 | 4.32 | - | - | 1.83 | 3.70 | 0.60 | 9 |
| TCO100 | 0.03 | -0.06 | -0.68 | 0.14 | - | -1.55 | - | 0.03 | - | -0.02 | 0.00 | -1.38 | 8 |
| TCO110 | 0.26 | 4.05 | 0.93 | 9.57 | - | 1.17 | 0.01 | 1.72 | - | 0.26 | 2.12 | -3.27 | 10 |
| TCO200 | 0.05 | 3.59 | -0.09 | 0.77 | - | -0.25 | - | 0.04 | - | -0.16 | 0.01 | -0.97 | 9 |
| TCO210 | -0.89 | -2.11 | 2.03 | 13.20 | - | 0.81 | - | 1.20 | - | 0.00 | 3.49 | -0.32 | 8 |
| *Percent Cover 1990- all plots* | | | | | | | | | | | | | |
| HJA100 | 0.90 | 0.11 | 6.18 | 0.59 | - | - | - | 0.23 | 0.15 | - | 0.55 | 0.43 | 8 |
| HJA110 | 0.07 | 0.20 | 3.64 | 0.31 | - | - | - | 0.17 | - | - | 0.14 | 0.39 | 7 |
| HJA200 | 0.58 | - | 3.72 | 0.29 | - | - | - | 1.53 | 1.45 | - | 0.17 | 0.65 | 7 |
| HJA210 | 0.03 | - | 1.95 | 0.08 | - | - | - | 0.29 | 8.97 | - | - | 0.08 | 5 |
| MCY 100 | 7.71 | 0.12 | 39.95 | - | - | 1.21 | - | - | - | 0.00 | 0.04 | 0.08 | 6 |
| MCY110 | 5.96 | - | 26.53 | - | - | 6.73 | - | - | - | 0.39 | 0.23 | 0.38 | 6 |
| MCY200 | 2.34 | - | 23.46 | - | - | 26.11 | - | - | - | 0.30 | 0.37 | 0.58 | 6 |
| MCY210 | 4.32 | 0.63 | 31.82 | - | - | 12.09 | - | - | - | 0.56 | 0.04 | 0.31 | 7 |
| PCM100 | 4.97 | 19.88 | 8.60 | - | - | 0.38 | - | 0.15 | - | 2.12 | 0.67 | 0.85 | 8 |
| PCM110 | 3.06 | 11.46 | 13.04 | 0.02 | - | 10.90 | - | 0.63 | - | 1.77 | 0.74 | 4.86 | 9 |
| PCM200 | 1.85 | 18.81 | 15.64 | 0.19 | - | 1.06 | 0.00 | - | - | 2.13 | 0.03 | 0.04 | 8 |

(continued)

**Table 10 (continued)**

| SITES | ACCI | ACTR | BENE | COCA | EPAN | GASH | LAMU | LIBO2 | RHMA | ROGY | RUUR | VAPA | total spp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PCM210 | 6.51 | 12.12 | 16.57 | - | - | 7.91 | - | - | - | 1.81 | 0.80 | 2.63 | 7 |
| TCO100 | 0.11 | 0.12 | 5.08 | 1.80 | - | 4.72 | - | 0.26 | - | 0.02 | 0.02 | 2.24 | 9 |
| TCO110 | 0.46 | 9.13 | 5.47 | 2.98 | - | 1.64 | - | 0.83 | - | 0.31 | 0.15 | 5.99 | 9 |
| TCO200 | - | 4.02 | 6.18 | 1.95 | - | 1.03 | - | 0.57 | - | 0.34 | 0.05 | 1.80 | 8 |
| TCO210 | 0.97 | 7.02 | 2.15 | 3.16 | - | 0.61 | - | 0.69 | - | 0.66 | 0.39 | 2.66 | 9 |
| Mean 1990 | 2.66 | 6.97 | 13.12 | 1.14 | - | 6.20 | 0.00 | 0.53 | 3.52 | 0.87 | 0.29 | 1.50 | 10 |
| *Percent Cover 1997- all plots* | | | | | | | | | | | | | |
| HJA100 | 1.68 | 0.12 | 6.40 | 1.10 | - | - | - | 0.61 | 0.17 | - | 0.68 | 0.39 | 8 |
| HJA110 | - | 0.38 | 6.15 | 0.51 | 4.04 | - | 0.49 | 1.71 | - | 0.28 | 7.29 | 1.05 | 9 |
| HJA200 | 0.81 | - | 2.12 | 0.19 | - | - | - | 1.53 | 2.86 | - | 0.03 | 0.20 | 7 |
| HJA210 | - | - | 3.42 | 0.45 | 5.57 | - | 2.11 | 4.92 | 3.53 | - | 4.71 | 1.45 | 8 |
| MCY100 | 8.11 | 0.06 | 29.62 | - | - | 1.22 | 0.02 | - | - | 0.03 | 0.05 | 0.03 | 8 |
| MCY110 | 13.77 | 0.00 | 30.10 | - | 0.05 | 20.97 | 2.49 | - | - | 0.48 | 7.57 | 0.15 | 8 |
| MCY200 | 3.67 | 0.02 | 23.05 | - | - | 12.88 | - | - | - | 0.04 | 0.30 | 0.16 | 7 |
| MCY210 | 10.94 | 0.63 | 32.65 | - | 0.00 | 22.53 | 0.30 | - | - | 1.83 | 6.94 | 0.21 | 8 |
| PCM100 | 4.72 | 23.80 | 6.65 | - | - | 0.48 | 0.02 | 0.13 | - | 1.36 | 0.59 | 0.77 | 9 |
| PCM110 | 6.40 | 17.47 | 10.49 | - | 0.12 | 9.89 | 1.06 | 1.90 | - | 2.33 | 4.31 | 4.16 | 10 |
| PCM200 | 1.67 | 21.78 | 12.51 | 0.03 | - | 1.56 | 0.03 | - | - | 1.85 | 0.09 | 0.04 | 9 |
| PCM210 | 17.42 | 18.28 | 7.48 | - | 0.09 | 8.82 | 4.32 | - | - | 3.64 | 4.50 | 3.22 | 9 |
| TCO100 | 0.15 | 0.06 | 4.40 | 1.94 | - | 3.17 | - | 0.28 | - | 0.00 | 0.01 | 0.85 | 8 |
| TCO110 | 0.73 | 13.18 | 6.39 | 12.55 | - | 2.81 | 0.01 | 2.55 | - | 0.56 | 2.26 | 2.72 | 10 |
| TCO200 | 0.05 | 7.60 | 6.09 | 2.72 | - | 0.78 | - | 0.61 | - | 0.18 | 0.07 | 0.82 | 9 |
| TCO210 | 0.08 | 4.91 | 4.18 | 16.35 | - | 1.42 | - | 1.89 | - | 0.66 | 3.87 | 2.34 | 9 |
| Mean 1997 | 5.01 | 7.74 | 11.98 | 3.98 | 1.64 | 7.21 | 1.09 | 1.61 | 2.19 | 1.02 | 2.70 | 1.16 | 12 |

**Figure 12:** Scatterplot of average cover values per study site for *Rubus ursinus* in 1990 and 1997. Plots above the 45 degree line increased from 1990 to 1997, while values below decreased in biomass (t=treatment, c=control, 1=primary, 2=secondary).

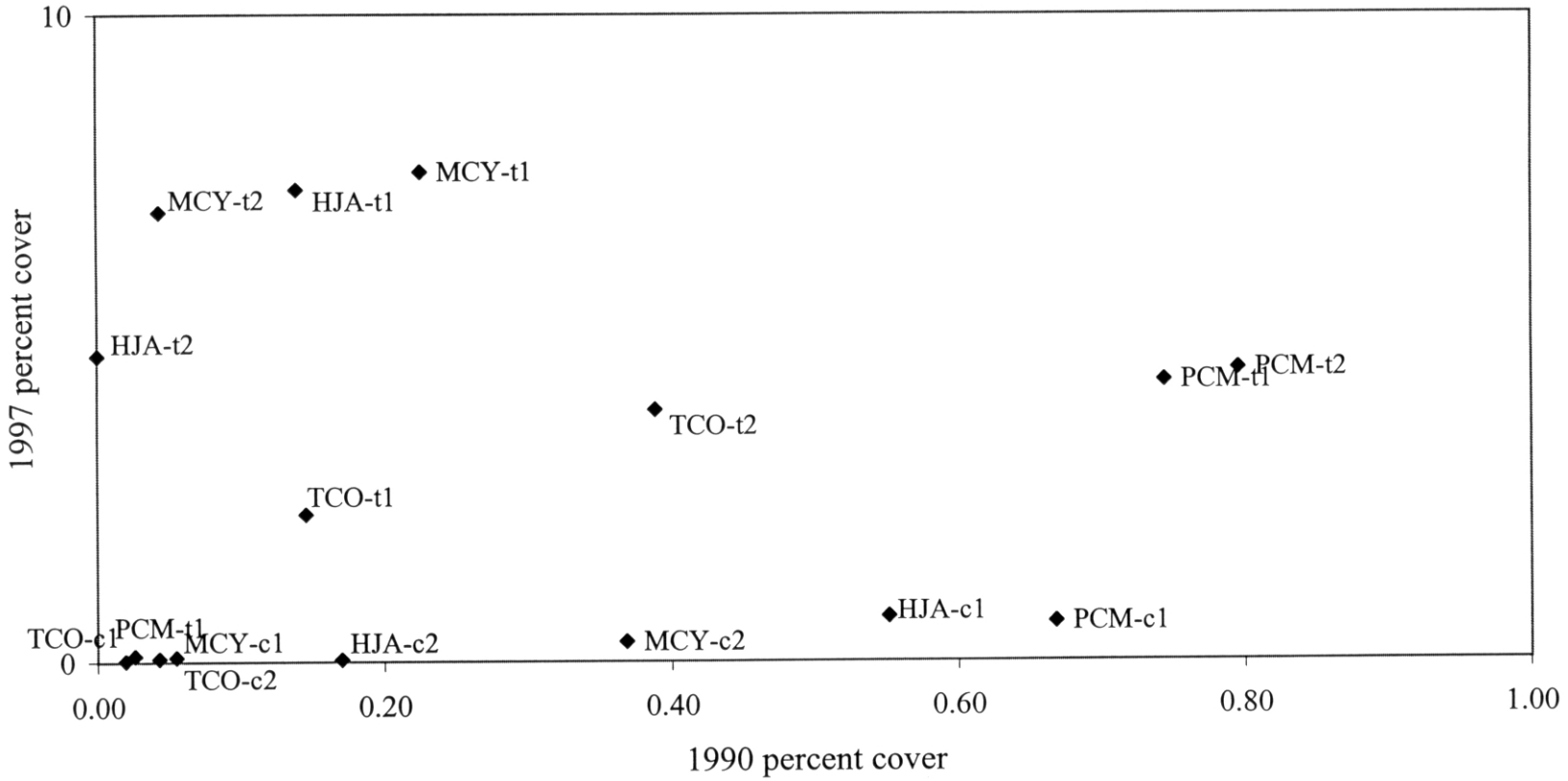


**Figure 13:** Scatterplot of average cover values per study site for *Berberis nervosa* in 1990 and 1997. Plots above the 45 degree line increased from 1990 to 1997, while values below decreased in biomass (t=treatment, c=control, 1=primary, 2=secondary).

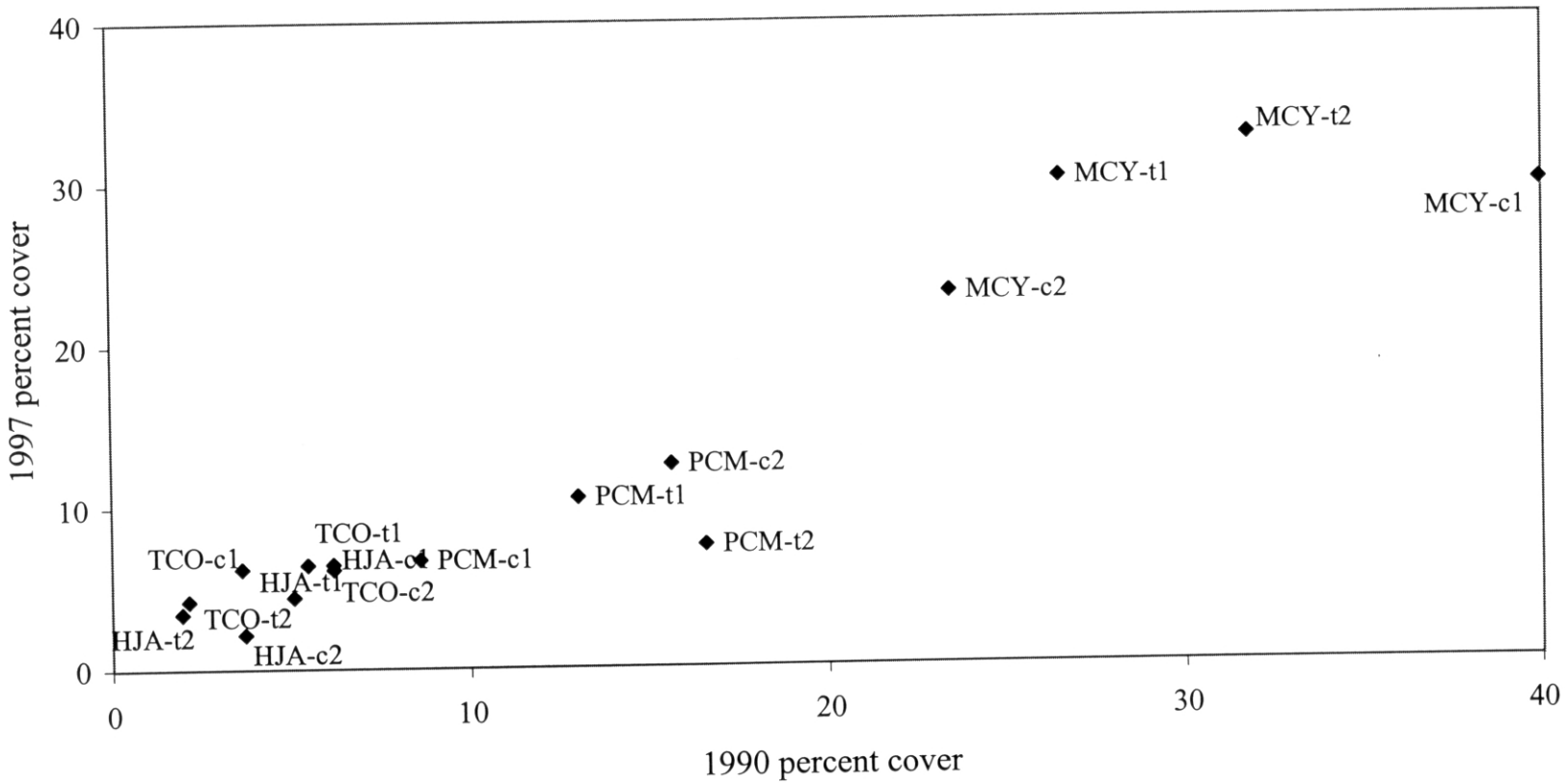


**Figure 14:** Scatterplot of average cover values per study site for *Vaccinium parvifolium* in 1990 and 1997. Plots above the 45 degree line increased from 1990 to 1997, while values below decreased in biomass (t=treatment, c=control, 1=primary, 2=secondary).

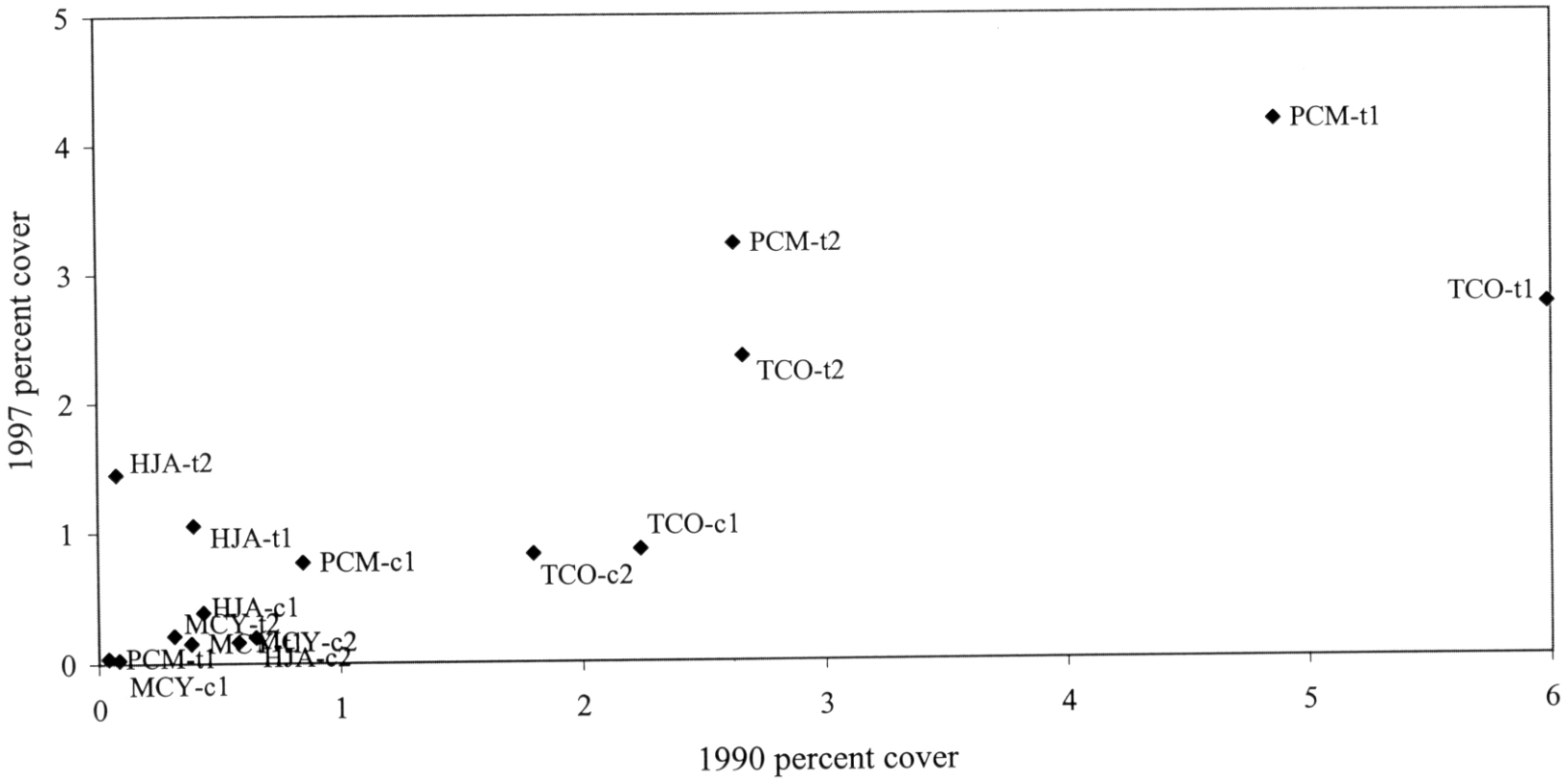


**Figure 15:** Scatterplot of average cover values per study site for *Gaultheria shallon* in 1990 and 1997. Plots above the 45 degree line increased from 1990 to 1997, while values below decreased in biomass (t=treatment, c=control, 1=primary, 2=secondary).

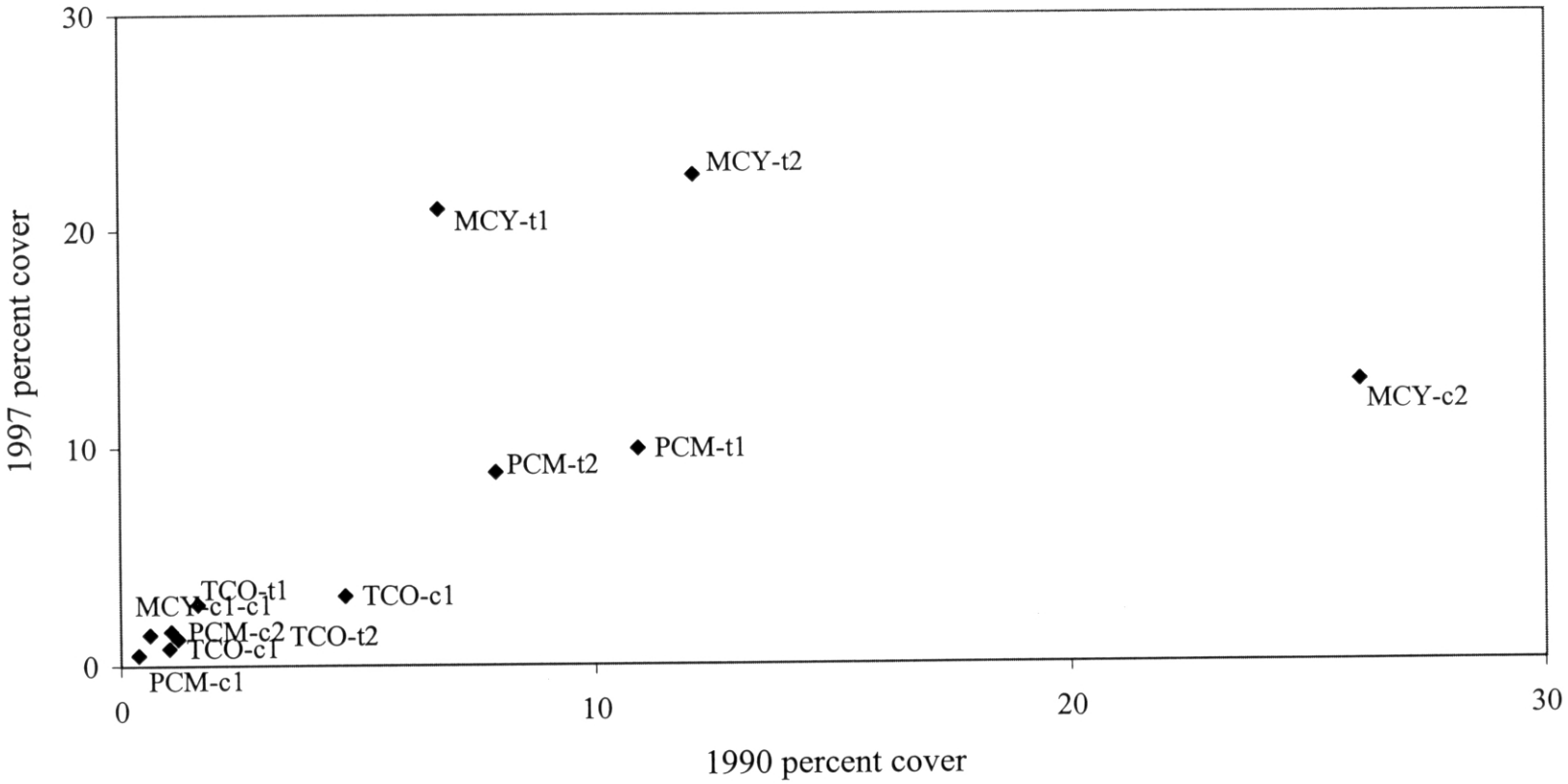


**Figure 16:** Scatterplot of average cover values per study site for *Cornus canadensis* in 1990 and 1997. Plots above the 45 degree line increased from 1990 to 1997, while values below decreased in biomass (t=treatment, c=control, 1=primary, 2=secondary).

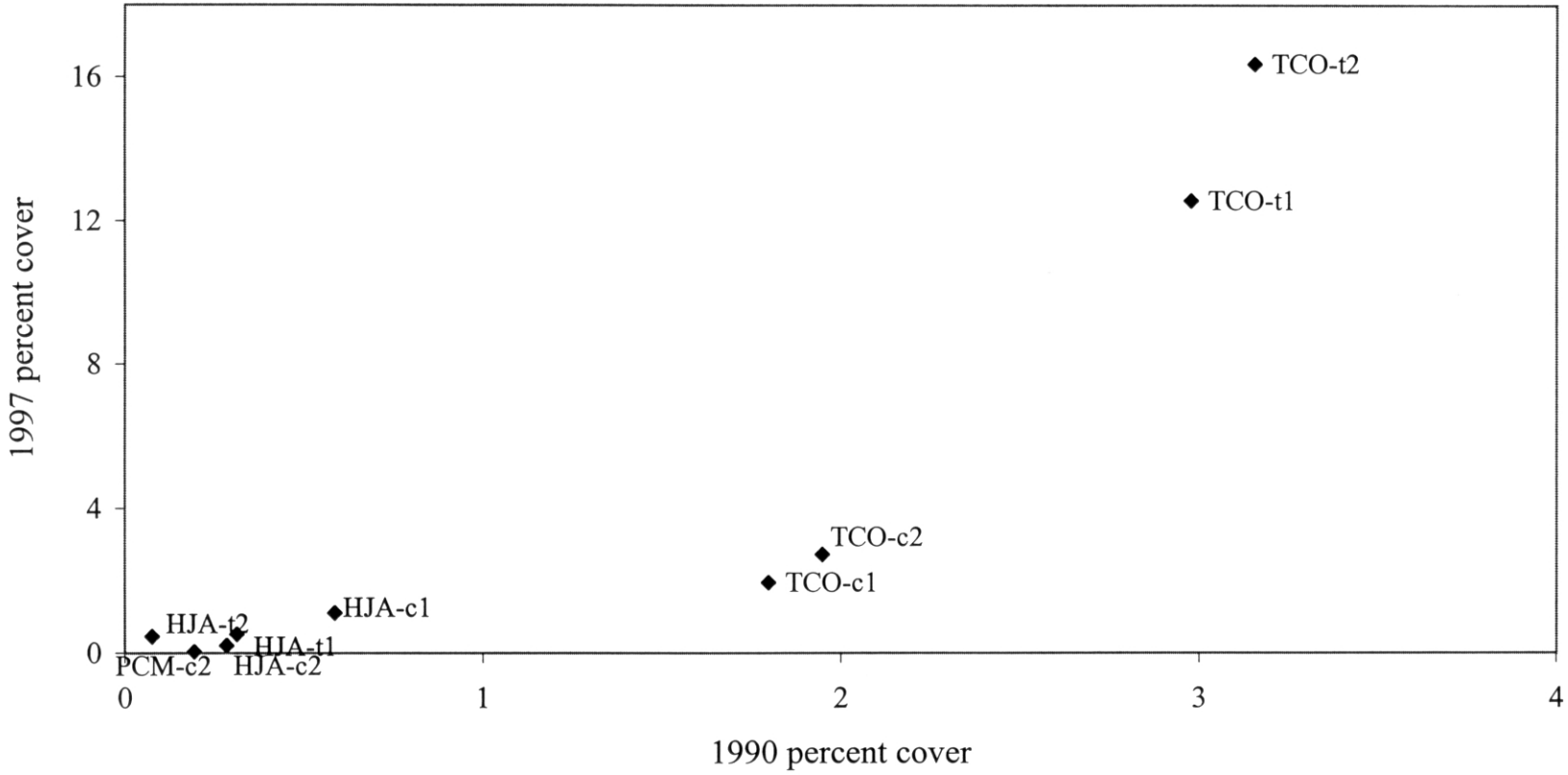
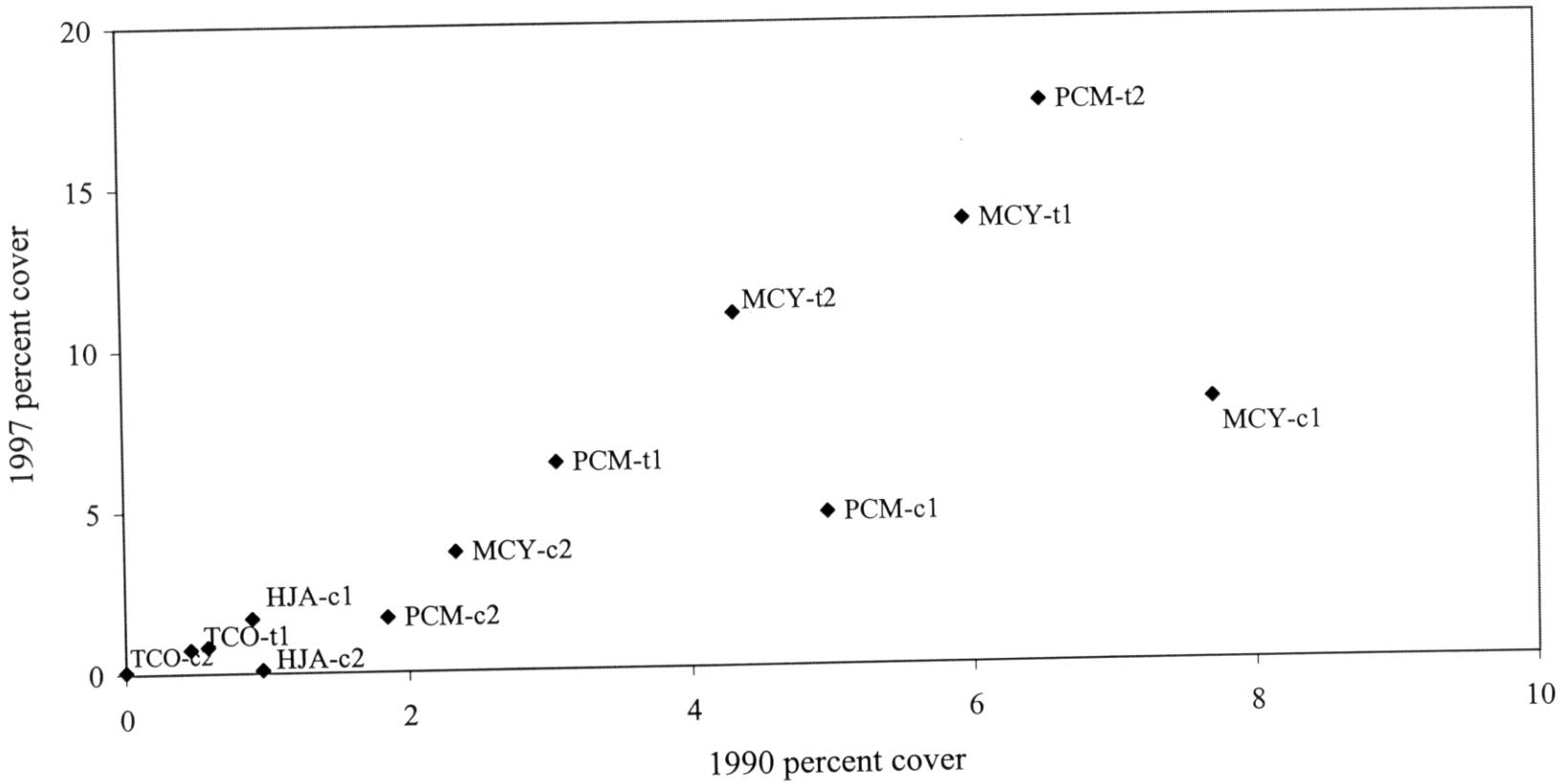


**Figure 17:** Scatterplot of average cover values per study site for *Acer cincinatum* in 1990 and 1997. Plots above the 45 degree line increased from 1990 to 1997, while values below decreased in biomass (t=treatment, c=control, 1=primary, 2=secondary).



10). These species had little or no cover in 1990 and the values of cover represent the amount present in 1997. The two herbaceous species, *Achlys triphylla* (Figure 18) and *Linnaea borealis* (Figure 19), behaved similarly in treatment plots by increasing slightly (neither were present at Martha Creek, nor was *Cornus canadensis*, another herbaceous species).

Species' responses in the control plots showed some variation between 1990 and 1997, though most species decreased slightly or did not change significantly, especially when compared to species' responses in treatment plots (Table 10). *Gaultheria shallon* and *Berberis nervosa* decreased the most in percent average cover from 1990 to 1997, with the greatest decline occurring at Martha Creek for both species (5.4% for *Berberis nervosa*, 6.6% for *Gaultheria shallon)*. *Achlys triphylla* had the greatest increase of percent average cover in the control plots (3.5% increase at Panther Creek and 1.8% increase at Trout Creek) (Figure 18).

Treatment and site are important variables for determining the amount of cover found for four species: *Acer cinncinatum*, *Cornus canadensis*, *Gaultheria shallon* and *Rubus ursinus* (Table 11) ($p < 0.0005$). Gap alone was an important variable for *Rosa gymnocarpa* as it increased in nine sites and was found in all four stands (Figure 20). *Rosa gymnocarpa* either decreased or had no change at four sites and was found in all stands except H.J. Andrews. Site is an important variable for *Epilobium angustifolium* because it was absent from all plots in 1990, and appeared in two of the four plots at H. J. Andrews and Panther Creek in 1997.

**Figure 18:** Percent average cover values per study site for *Achlys triphylla* in 1990 and 1997. Plots above the 45 degree line increased from 1990 to 1997, while values below decreased in biomass (t=treatment, c=control, 1=primary, 2=secondary).

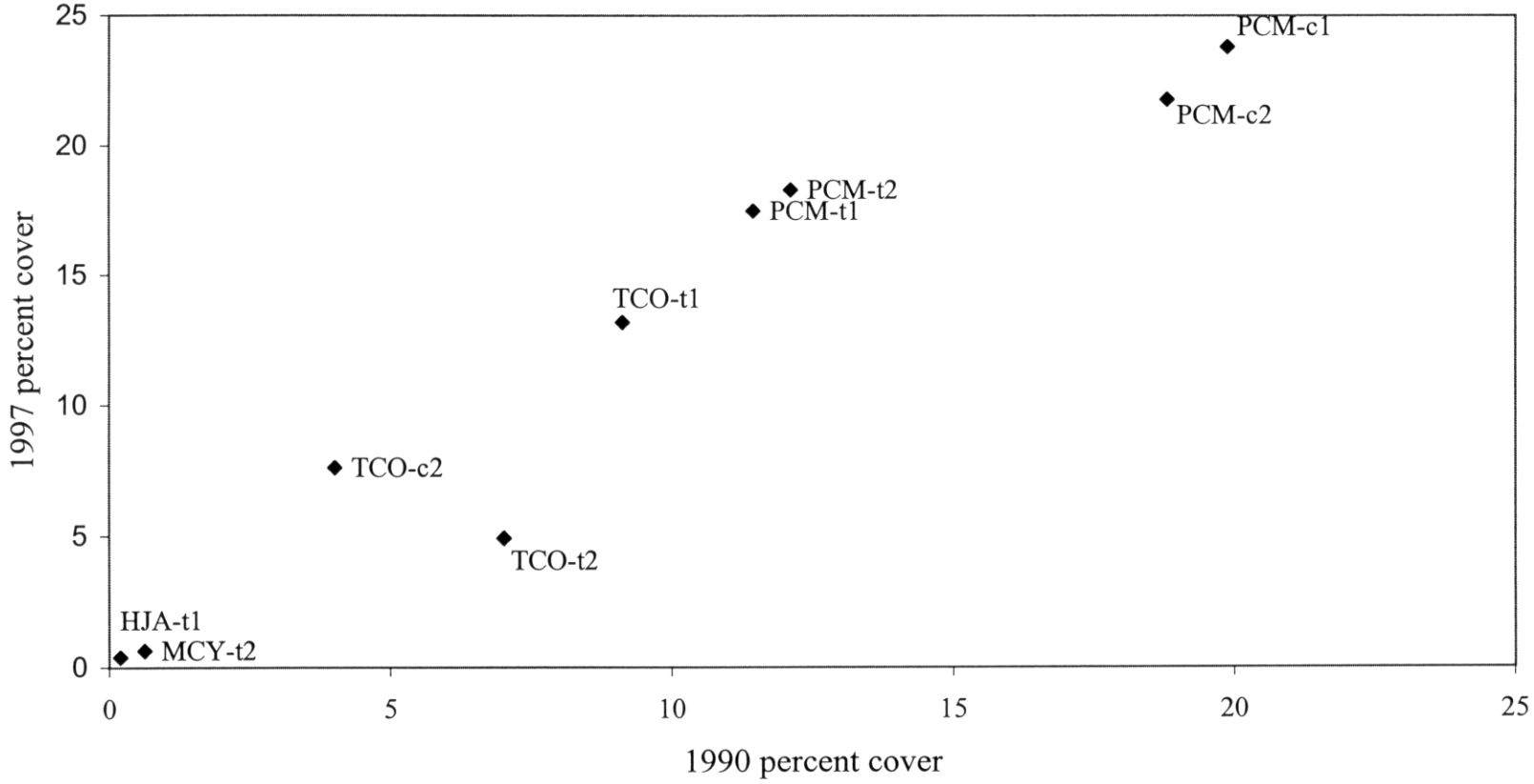


**Figure 19:** Scatterplot of average cover values per study site for *Linnaea borealis* in 1990 and 1997. Plots above the 45 degree line increased from 1990 to 1997, while values below decreased in biomass (t=treatment, c=control, 1=primary, 2=secondary).

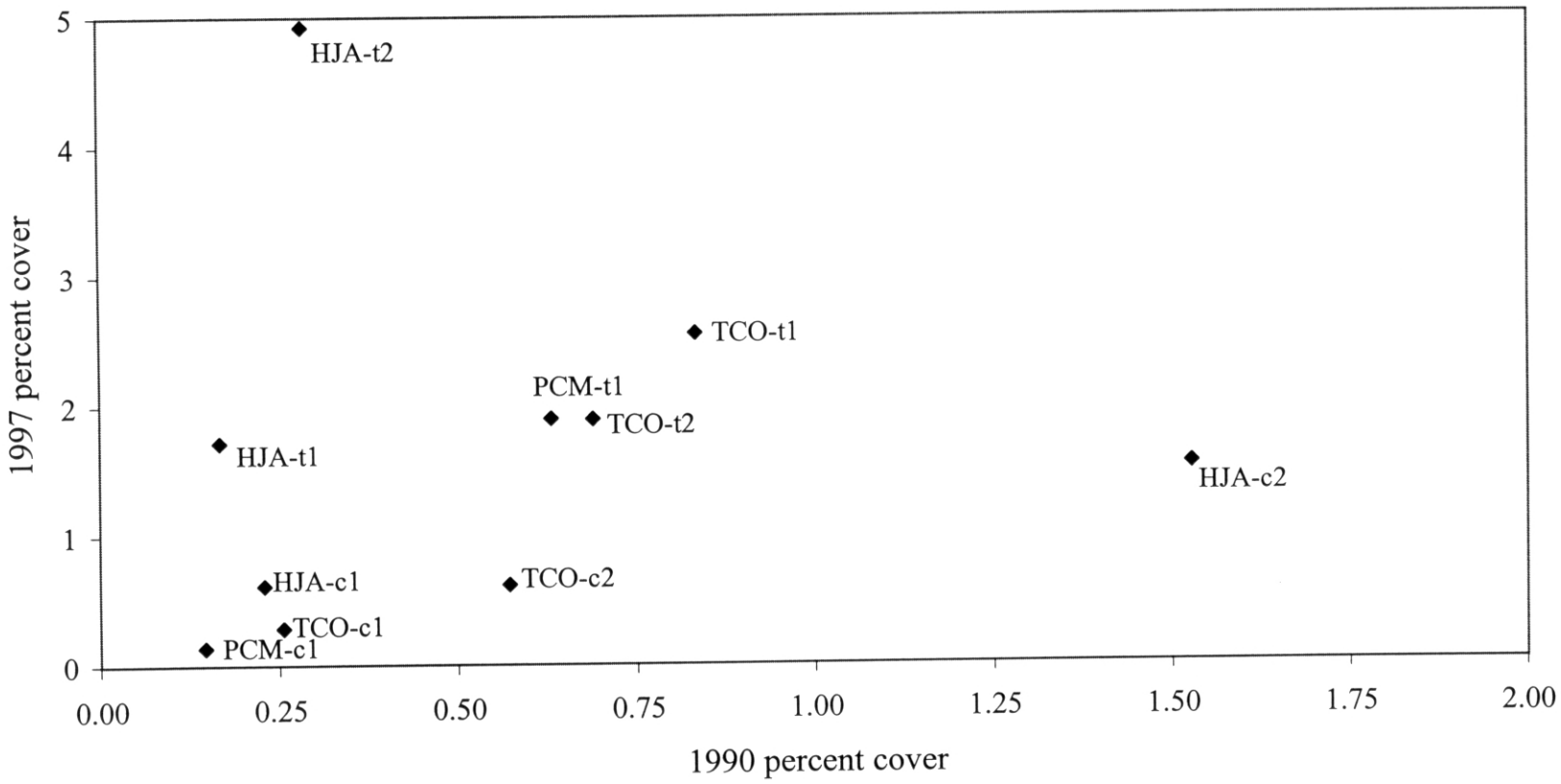


**Table 11:** Results of General Linear Model for percent average cover for individual species at 16 sites (two treatment, two control, at each of four sites) using an interaction model. Factor abbrevations are: GAP = treated site (vs. control) and SITE = location.

| Dependent Variable | Independent Variable | df | Type III SS | MSE | F | P | R-Square |
|---|---|---|---|---|---|---|---|
| 1 *Acer cinncinatum (ACCI)* | | 7 | 150.33 | 21.48 | 5.61 | 0.0360 | 0.83 |
| | GAP | 1 | 40.79 | 40.79 | 10.65 | 0.0115 | |
| | SITE | 3 | 55.82 | 18.61 | 4.86 | 0.0328 | |
| | GAP*SITE | 3 | 53.72 | 17.91 | 4.86 | 0.0360 | |
| 2 *Achlys triphylla (ACTR)* | | 7 | 62.53 | 8.93 | 2.05 | 0.1995 | 0.71 |
| | GAP | 1 | 0.84 | 0.84 | 0.19 | 0.6761 | |
| | SITE | 3 | 54.89 | 18.30 | 4.21 | 0.0637 | |
| | GAP*SITE | 3 | 6.53 | 2.18 | 0.50 | 0.6954 | |
| 3 *Berberis nervosa (BENE)* | | 7 | 140.57 | 20.08 | 2.05 | 0.1671 | 0.64 |
| | GAP | 1 | 19.54 | 19.54 | 2.00 | 0.1951 | |
| | SITE | 3 | 61.88 | 20.63 | 2.11 | 0.1772 | |
| | GAP*SITE | 3 | 59.15 | 19.72 | 2.02 | 0.1901 | |
| 4 *Cornus canadensis (COCA)* | | 5 | 199.98 | 40.00 | 22.95 | 0.0048 | 0.96 |
| | GAP | 1 | 31.14 | 31.14 | 17.87 | 0.0134 | |
| | SITE | 2 | 80.48 | 40.24 | 23.09 | 0.0064 | |
| | GAP*SITE | 2 | 70.37 | 35.18 | 20.19 | 0.0081 | |

(continued)

**Table 11 (continued)**

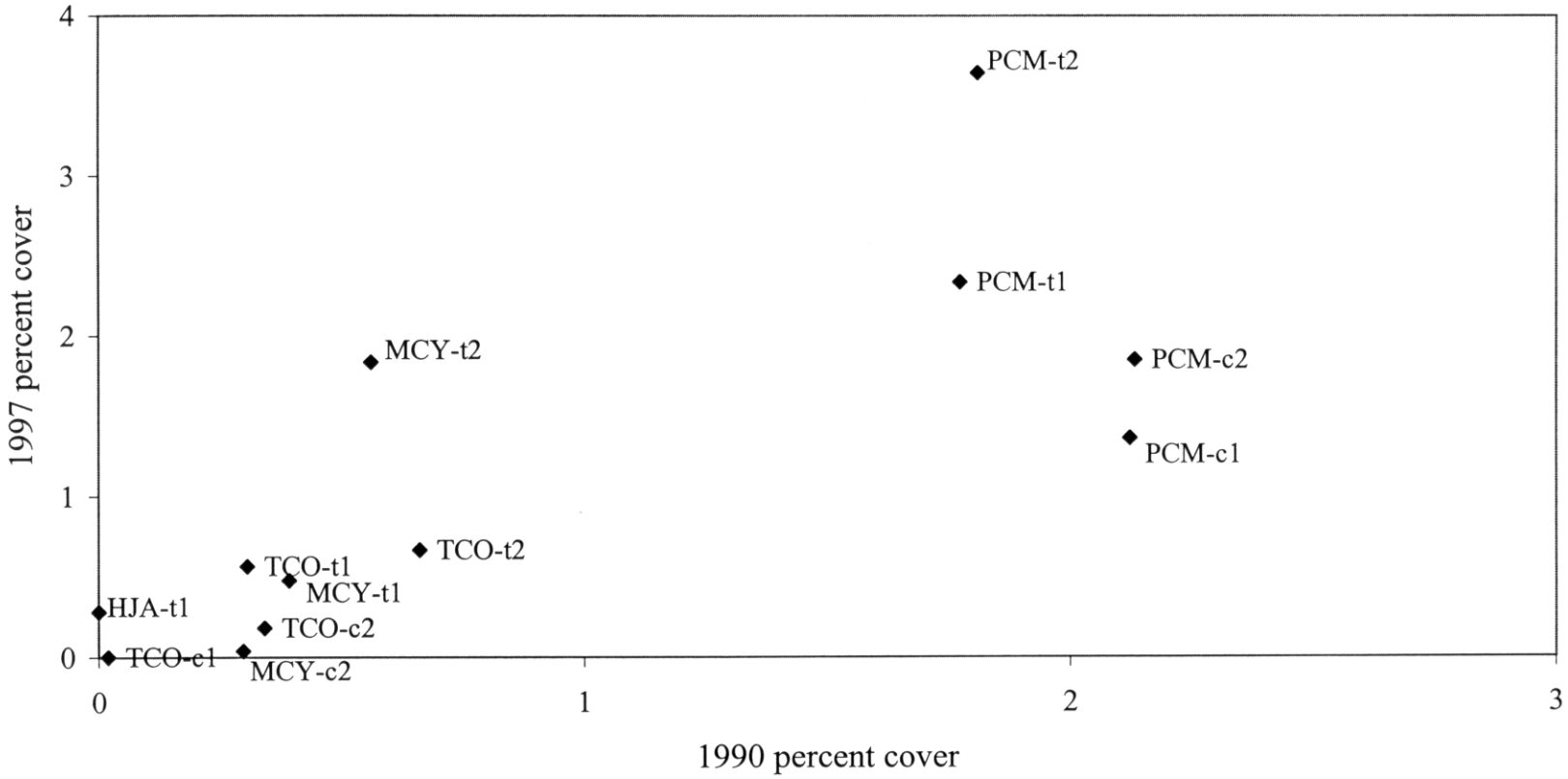
| Dependent Variable | Independent Variable | df | Type III SS | MSE | F | P | R-Square |
|---|---|---|---|---|---|---|---|
| 5 *Epilobium angustifolium (EPAN)* | | 2 | 29.98 | 14.99 | 38.23 | 0.0073 | 0.96 |
| | GAP | 0 | 0.00 | - | - | - | |
| | SITE | 2 | 29.98 | 14.99 | 38.23 | 0.0073 | |
| | GAP*SITE | 0 | 0.00 | - | - | - | |
| 6 *Gaultheria shallon (GASH)* | | 5 | 383.32 | 76.66 | 4.71 | 0.0429 | 0.80 |
| | GAP | 1 | 139.88 | 139.88 | 8.59 | 0.0262 | |
| | SITE | 2 | 20.64 | 10.31 | 0.63 | 0.5627 | |
| | GAP*SITE | 2 | 222.80 | 111.40 | 6.84 | 0.0283 | |
| 7 *Lactuca muralis* | | 5 | 10.00 | 2.00 | 0.89 | 0.5617 | 0.52 |
| | GAP | 1 | 6.54 | 6.54 | 2.90 | 0.1637 | |
| | SITE | 3 | 4.16 | 1.38 | 0.61 | 0.6407 | |
| | GAP*SITE | 1 | 0.66 | 0.67 | 0.30 | 0.6156 | |
| 8 *Linnaea borealis (LIBO)* | | 5 | 13.38 | 2.68 | 2.15 | 0.2395 | 0.73 |
| | GAP | 1 | 7.84 | 7.84 | 6.29 | 0.0662 | |
| | SITE | 2 | 2.13 | 1.06 | 0.85 | 0.4915 | |
| | GAP*SITE | 2 | 1.40 | 0.70 | 0.56 | 0.6095 | |
| 9 *Rosa gymnocarpa (ROGY)* | | 6 | 3.87 | 0.65 | 2.26 | 0.1725 | 0.69 |
| | GAP | 1 | 2.50 | 2.50 | 8.73 | 0.0255 | |
| | SITE | 3 | 0.35 | 0.12 | 0.41 | 0.7501 | |
| | GAP*SITE | 2 | 1.15 | 0.57 | 2.00 | 0.2157 | |

(continued)

**Table 11 (continued)**

| | Dependent Variable | Independent Variable | df | Type III SS | MSE | F | P | R-Square |
|---|---|---|---|---|---|---|---|---|
| 10 | *Rubus ursinus (RUUR)* | | 7 | 119.24 | 17.03 | 33.44 | 0.0001 | 0.97 |
| | | GAP | 1 | 95.28 | 95.28 | 187.07 | 0.0001 | |
| | | SITE | 3 | 11.81 | 3.94 | 7.73 | 0.0095 | |
| | | GAP*SITE | 3 | 12.14 | 1.05 | 7.95 | 0.0088 | |
| 11 | *Vaccinium parviflora (VAPA)* | | 7 | 9.73 | 1.39 | 1.96 | 0.1831 | 0.63 |
| | | GAP | 1 | 0.12 | 0.13 | 0.18 | 0.6855 | |
| | | SITE | 3 | 7.75 | 2.58 | 3.64 | 0.0639 | |
| | | GAP*SITE | 3 | 7.86 | 0.62 | 0.87 | 0.4947 | |

**Figure 20:** Scatterplot of average cover values per study site for *Rosa gymnocarpa* in 1990 and 1997. Plots above the 45 degree line increased from 1990 to 1997, while values below decreased in biomass (t=treatment, c=control, 1=primary, 2=secondary).



## 3.5 Dominance and Diversity Patterns

The expected dominance diversity curve was for old-growth plots to have less dominance (cover) than mature stands, but high diversity and mature plots to have high dominance compared to old-growth stands, but low diversity. The actual outcome only partly fit this model (Figure 21). In 1990 and 1997, H.J. Andrews, an old-growth site, had low dominance and high diversity, while Martha Creek had high dominance, but low diversity. Trout Creek also fit the old-growth model in 1990, while Panther Creek, a mature site, did not fall clearly into either pattern. In 1997, Vegetation responses at Panther Creek and Trout Creek were similar, despite the difference in age class at these sites.

The number of species (diversity) increased at all sites from 1990 to 1997 (Table 12). From 1990 to 1997, the greatest increase in diversity occurred at Martha Creek (12 species in 1990, 38 species in 1997). Martha Creek was followed by H.J. Andrews (26 species in 1990, 51 species in 1997), Panther Creek (45 species in 1990, greater than 57 species in 1997) and Trout Creek (30 species in 1990, 41 species in 1997). Panther Creek had greater diversity in 1990 and 1997 than any site, despite being a mature site. Martha Creek had the least diversity in both years.

Although the number of species to increase from 1990 to 1997 differed only slightly between mature stands and old-growth stands, the type of species found (such as herbs, shrubs or trees) differed greatly (Table 12). In 1997, tree seedlings

Figure 21: Dominance/Diversity Curve including all species at treated sites in 1990 and 1997.

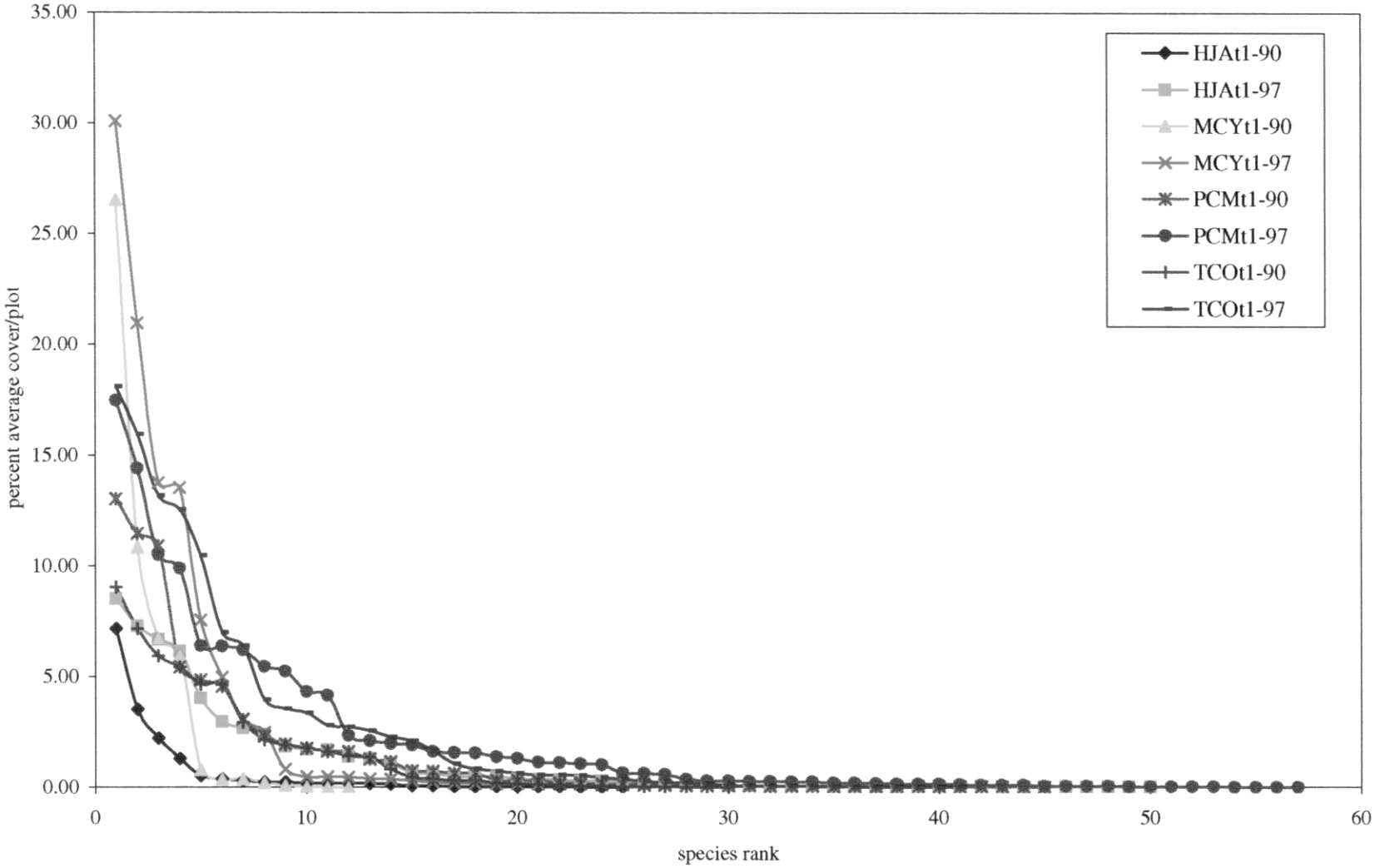


Table 12: Mean average cover of understory species in primary treatment plots. All species found at a study site are ranked and listed by forest service code by dominant species for each year, 1990 and 1997. H = H. J.Andrews, M = Martha Creek, P = Panther Creek, and T = Trout Creek. Species with 0 values indicate trace amounts.

| | spp | H90 | spp | H97 | spp | M90 | spp | M97 | spp | P90 | spp | P97 | spp | T90 | spp | T97 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | MOSS | 7 | MOSS | 9 | BENE | 27 | BENE | 30 | BENE | 13 | ACTR | 17 | ACTR | 9 | MOSS | 18 |
| 2 | BENE | 4 | RUUR | 7 | MOSS | 11 | GASH | 21 | ACTR | 11 | PTAQ | 14 | ABAM | 7 | ABAM | 16 |
| 3 | COLA | 2 | TSHE | 7 | GASH | 7 | ACCI | 14 | GASH | 11 | BENE | 10 | VAPA | 6 | ACTR | 13 |
| 4 | TSHE | 1 | BENE | 6 | ACCI | 6 | MOSS | 14 | XETE | 5 | GASH | 10 | BENE | 5 | COCA | 13 |
| 5 | POMU | 1 | EPAN | 4 | POMU | 1 | RUUR | 8 | VAPA | 5 | ACCI | 6 | VAAL | 5 | VAAL | 10 |
| 6 | VAPA | 0 | COLA | 3 | ROGY | 0 | RULE | 5 | PTAQ | 5 | XETE | 6 | MOSS | 5 | TSHE | 7 |
| 7 | COCA | 0 | POMU | 3 | VAPA | 0 | POMU | 3 | ACCI | 3 | MOSS | 6 | COCA | 3 | BENE | 6 |
| 8 | VISE | 0 | TITR | 2 | RUUR | 0 | LAMU | 2 | VAHE | 2 | VAHE | 5 | TSHE | 2 | CLUN | 4 |
| 9 | TITR | 0 | TRLA2 | 2 | VISE | 0 | ATFI | 1 | MOSS | 2 | ANDE | 5 | VAME | 2 | TITR | 4 |
| 10 | GOOB | 0 | LIBO2 | 2 | CHME | 0 | ROGY | 0 | ROGY | 2 | RUUR | 4 | CLUN | 2 | VAHE | 3 |
| 11 | ACTR | 0 | VISE | 2 | TROV | 0 | PSME | 0 | VISE | 2 | VAPA | 4 | GASH | 2 | GASH | 3 |
| 12 | RUNI | 0 | HIAL | 1 | TSHE | 0 | TSHE | 0 | ANDE | 2 | ROGY | 2 | VAHE | 1 | VAPA | 3 |
| 13 | LIBO2 | 0 | RUNI | 1 | | | VISE | 0 | CHUM | 1 | VISE | 2 | CHUM | 1 | LIBO2 | 3 |
| 14 | RUUR | 0 | VAPA | 1 | | | TRLA2 | 0 | HODI | 1 | LONIC | 2 | LIBO2 | 1 | RUUR | 2 |
| 15 | ACCI | 0 | PSME | 1 | | | HIAL | 0 | RUUR | 1 | LIBO2 | 2 | ACCI | 0 | VAME | 2 |
| 16 | ANDE | 0 | RULE | 1 | | | ADBI | 0 | ADBI | 1 | HODI | 2 | TITR | 0 | CHUM | 2 |
| 17 | VAHE | 0 | COCA | 1 | | | GATR | 0 | LIBO2 | 1 | TRLA2 | 2 | VAXX | 0 | PSME | 1 |
| 18 | TRLA2 | 0 | LAMU | 0 | | | PTAQ | 0 | LAPO | 1 | CONU | 2 | ROGY | 0 | VISE | 1 |
| 19 | CHME | 0 | THPL | 0 | | | LAPO | 0 | TRLA2 | 0 | ADBI | 1 | XETE | 0 | ACCI | 1 |
| 20 | PYSE | 0 | ACTR | 0 | | | PREM | 0 | ACGL | 0 | CHUM | 1 | RUUR | 0 | SYMPH | 1 |
| 21 | VAME | 0 | RULA | 0 | | | CIRSI | 0 | SYMPH | 0 | SYMPH | 1 | VISE | 0 | ROGY | 1 |
| 22 | CHUM | 0 | VAME | 0 | | | VAPA | 0 | RUPA | 0 | RUPA | 1 | TROV | 0 | RULE | 1 |

(continued)

**Table 12 (continued)**

| | spp | H90 | spp | H97 | spp | M90 | spp | M97 | spp | P90 | spp | P97 | spp | T90 | spp | T97 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **23** | VAXX | 0 | VAHE | 0 | | | XETE | 0 | SMST | 0 | LAMU | 1 | PTAQ | 0 | RUNI | 1 |
| **24** | ASCA3 | 0 | ATFI | 0 | | | ACMA | 0 | COCOC | 0 | LAPO | 1 | RULA | 0 | PTAQ | 0 |
| **25** | PSME | 0 | ROGY | 0 | | | CASC2 | 0 | VAME | 0 | HIAL | 1 | ANDE | 0 | ATFI | 0 |
| **26** | COCOC | 0 | EPWA | 0 | | | DIHO | 0 | CONU | 0 | GRAMI | 1 | SMST | 0 | HIAL | 0 |
| **27** | | | ASCA3 | 0 | | | GRAMI | 0 | PYSE | 0 | OSCH | 1 | SYMPH | 0 | XETE | 0 |
| **28** | | | CIRSI | 0 | | | RUPA | 0 | GOOB | 0 | PSME | 0 | GOOB | 0 | VAXX | 0 |
| **29** | | | GRAMI | 0 | | | VEWO | 0 | TROV | 0 | ACGL | 0 | LICA3 | 0 | TROV | 0 |
| **30** | | | RUAC | 0 | | | ASTER1 | 0 | ANLY2 | 0 | VAME | 0 | CHME | 0 | POMU | 0 |
| **31** | | | ANMA | 0 | | | FRAGA | 0 | CLUN | 0 | PYSE | 0 | | | FRAGA | 0 |
| **32** | | | CAREX | 0 | | | EPAN | 0 | AMAL | 0 | TROV | 0 | | | ANDE | 0 |
| **33** | | | PREM | 0 | | | TROV | 0 | PERA | 0 | AMAL | 0 | | | SMST | 0 |
| **34** | | | SENEC | 0 | | | SARA | 0 | LICO3 | 0 | SPBE | 0 | | | SENEC | 0 |
| **35** | | | ANDE | 0 | | | OSCH | 0 | SPBE | 0 | SMST | 0 | | | RULA | 0 |
| **36** | | | CHUM | 0 | | | LONIC | 0 | TSHE | 0 | PYAS | 0 | | | GRAMI | 0 |
| **37** | | | EPPA | 0 | | | CONU | 0 | PYPI | 0 | POMU | 0 | | | LAMU | 0 |
| **38** | | | GOOB | 0 | | | LUPIN | 0 | CASC2 | 0 | CESA | 0 | | | ABPR | 0 |
| **39** | | | BLSP | 0 | | | | | PYAS | 0 | VAXX | 0 | | | ARENA | 0 |
| **40** | | | SARA | 0 | | | | | COCA | 0 | TITR | 0 | | | BLSP | 0 |
| **41** | | | PYSE | 0 | | | | | PIMO | 0 | EPAN | 0 | | | EPWA | 0 |
| **42** | | | VAXX | 0 | | | | | LICA3 | 0 | GATR | 0 | | | | |
| **43** | | | CLUN | 0 | | | | | GRAMI | 0 | COCOC | 0 | | | | |
| **44** | | | PYAS | 0 | | | | | TITR | 0 | GAOV | 0 | | | | |
| **45** | | | VAAL | 0 | | | | | GATR | 0 | ATFI | 0 | | | | |
| **46** | | | CACH | 0 | | | | | | | EPWA | 0 | | | | |
| **47** | | | FRAGA | 0 | | | | | | | ANMA | 0 | | | | |

(continued)

**Table 12 (continued)**

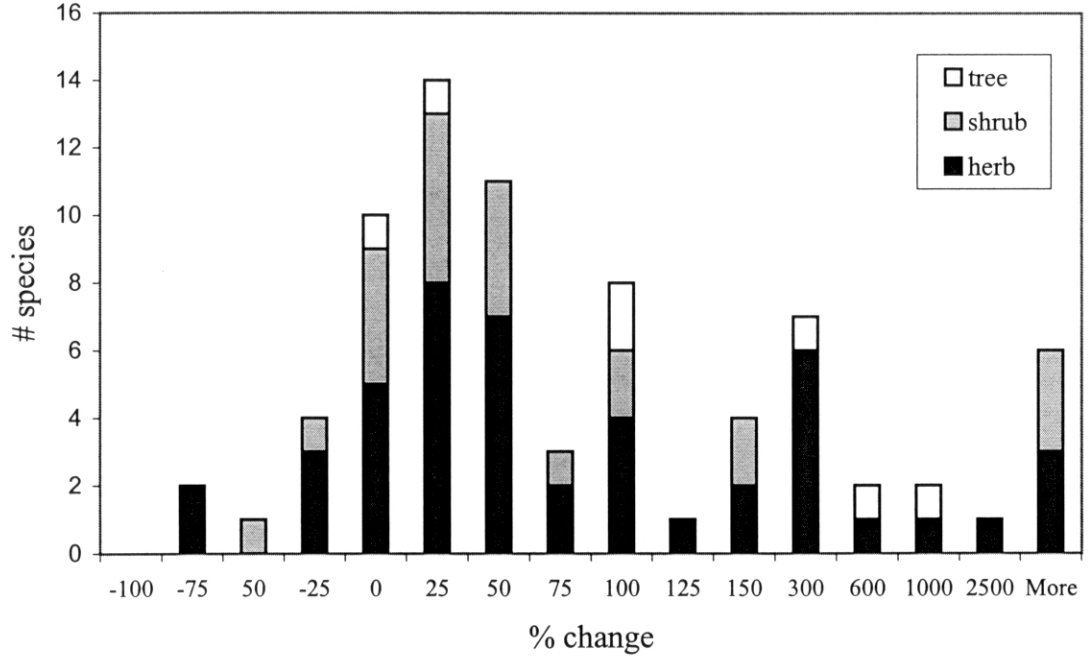
| | spp | H90 | spp | H97 | spp | M90 | spp | M97 | spp | P90 | spp | P97 | spp | T90 | spp | T97 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **48** | | | TROV | 0 | | | | | | | FRAGA | 0 | | | | |
| **49** | | | CASC2 | 0 | | | | | | | DIHO | 0 | | | | |
| **50** | | | GATR | 0 | | | | | | | PERA | 0 | | | | |
| **51** | | | ABAM | 0 | | | | | | | PYPI | 0 | | | | |
| **52** | | | | | | | | | | | CASC2 | 0 | | | | |
| **53** | | | | | | | | | | | GOOB | 0 | | | | |
| **54** | | | | | | | | | | | COHE | 0 | | | | |
| **55** | | | | | | | | | | | ABAM | 0 | | | | |
| **56** | | | | | | | | | | | PAMY | 0 | | | | |
| **57** | | | | | | | | | | | LICA3 | 0 | | | | |

ranked in the top ten most dominant species for old-growth sites, but did not rank in the top ten for mature sites. Moss values were also high for all stands, but greater in the old-growth stands. For instance, the two most dominant species in Trout Creek in 1997 were moss, which is typical of old-growth stands and moist soils, and *Abies amabilis*, a tree species.

Shrubs dominate the top-ranked species in the mature stands, with the exception of the herb *Achlys triphylla* at Panther Creek. For example, *Berberis nervosa* is highly ranked at all stands for both years and is especially abundant in the mature stands. *Gaultheria shallon* is prominent at Martha Creek and Panther Creek, with less prominence at Trout Creek. From 1990 to 1997, the trailing shrub *Rubus ursinus* increased in importance at all sites with greatest diversity at Martha Creek and H.J. Andrews.

Another indicator of species dominance and diversity is the percent change in the frequency of species occurrence (Figure 22). Percent change in the frequency of species occurrence from 1990 to 1997 ranged from less than 100% to greater than 2500% with no difference between trees, shrubs and herbs. Most of the change in species occurrence was positive and was in the 25-50% increase range with additional clusters of species showing averages of 100, 300 and greater than 2500%. Percent change in the frequency of occurrence of the 12 target species ranged from 6% to greater than 2500 % (Table 13). The frequency of the two herbaceous weedy species, *Lactuca muralis* and *Epilobium angustifolium,* increased more than 2000 % from 1990 to 1997. The only species to decrease was

**Figure 22:** Distribution of percent change in numbers of occurrences, by groups of species from 1990 to 1997. Including 76 species at all study sites and based on the formula: [(count97-count90)/count90].*




| % change | herb | shrub | tree |
|---|---|---|---|
| -100 | 0 | 0 | 0 |
| -75 | 2 | 0 | 0 |
| 50 | 0 | 1 | 0 |
| -25 | 3 | 1 | 0 |
| 0 | 5 | 4 | 1 |
| 25 | 8 | 5 | 1 |
| 50 | 7 | 4 | 0 |
| 75 | 2 | 1 | 0 |
| 100 | 4 | 2 | 2 |
| 125 | 1 | 0 | 0 |
| 150 | 2 | 2 | 0 |
| 300 | 6 | 0 | 1 |
| 600 | 1 | 0 | 1 |
| 1000 | 1 | 0 | 1 |
| 2500 | 1 | 0 | 0 |
| More** | 3 | 3 | 0 |
| total sps | 46 | 23 | 7 |

* There are 115 possible species, but those not found in 1990 were not inlcuded in the analysis.
** trace, if any, found in 1990

**Table 13:** Percent change in frequency of occurrence for the 12 target species from 1990 to 1997, using the formula: [(count97-count90)/count90].

| Code | Genera and Species | Common Name | % change |
|---|---|---|---|
| Herbs | | | |
| ACTR | *Achlys triphylla* | vanilla leaf | 14 |
| COCA | *Cornus canadensis* | bunchberry | 7 |
| EPAN | *Epilobium angustifolium* | fireweed | >2500 |
| LAMU | *Lactuca muralis* | wall lettuce | 2200 |
| LIBO2 | *Linnaea borealis* | western twinflower | 12 |
| Shrubs | | | |
| ACCI | *Acer cincinatum* | vine maple | 39 |
| BENE | *Berberis nervosa* | Oregon grape | 4 |
| GASH | *Gaultheria shallon* | salal | 21 |
| RHMA | *Rhododendron macrophyllum* | Rhododendron | 13 |
| ROGY | *Rosa gymnocarpa* | baldhip rose | 16 |
| RUUR | *Rubus ursinus* | Pacific blackberry | 135 |
| VAPA | *Vaccinium parvifolium* | red blueberry | -16 |

the shrub *Vaccinium parvifolium*. Among woody species the shrub *Rubus ursinus* had the greatest increase in frequency (135%).

# 4. DISCUSSION

## 4.1 Edge Importance

As this was an experimental study, it is safe to infer that gap creation will lead to a greater increase in plant cover at gap centers than at gap edges, despite a wide range in initial conditions. Although all sites increased in cover, the amount of increase was site specific and a function of conditions in 1990.

The greatest increase in the amount of edge cover occurred at H.J. Andrews, an old-growth site. This was also the site with the least amount of gap and edge cover in 1990, which may help explain why H.J. Andrews increased in 1997; there was simply more space for species to grow, in addition to an increase of light due to gap creation.

The vegetation cover responses in the edges at all three Wind River sites was negligible, while the gap results varied. Trout Creek and Panther Creek behaved similarly at both edges and gaps, despite the fact that Trout Creek is an old-growth stand and Panther Creek is a mature stand. This may be due to variables not included in this study, such as colder temperatures at Trout Creek and Panther Creek or more ground moisture.

Martha Creek, a mature stand, had the greatest variation and percent cover over all. *Gaultheria shallon* (salal) increased dramatically between 1990 to 1997 at Martha Creek, which is the major source of the increase. Interestingly, salal was not found at H.J. Andrews, it was rarely found at the other two Wind River sites,

and it decreased at the two control sites in Martha Creek. A trampling effect due to elk may contribute to the decrease in salal at Martha Creek. In addition, salal is more common on drier, less productive sites (Halpern and Spies 1995), as well as one of the key competitors with Douglas Fir (*Pseudotsuga menziesii*) during seedling establishment (Messier 1990). Since salal can shade out tree seedlings like *Pseudotsuga menziesii*, the response of salal to treatment may be important for forest managers interested in maximizing *Pseudotsuga menziesii* seedling establishment.

## 4.2 Control/Treatment Importance

A "treatment effect" was evident in all analyses in that average understory vegetation cover increased more in the gaps than the controls. The increase in cover in the gaps was probably due to a greater accessibility of resources such as light and moisture. The controls either stayed the same or decreased, probably due to a lesser accessibility of resources. Pre-treatment conditions in 1990 were not an important variable in determining the percent cover in 1997, but they were important for determining the amount of biomass in 1997. This difference may be caused by only using 12 species for cover estimates, which limits the degrees of freedom in the model.

The difference in percent cover is dependent upon an interaction effect of treatment and gap. This mean that cover may have varying effects, depending on

which site is being examined. Biomass did not have an interaction effect, which means treatment (gap creation) will affect biomass at all sites and it is not site dependent. The biomass analysis included more species and had a greater sampling population than percent cover of understory vegetation, but did not separate gap edges from gap centers, which may bias the results.

Although site was not statistically significant in any of the models, it is still important to examine the differences between old-growth sites and mature sites since tree gaps are important transition areas from mature to old-growth forests (Spies and Franklin 1989). In this study, six growing seasons after gap creation, understory characteristics depended on the stands' age-class at the time of treatment. Old-growth sites initially had the resources (shade and moisture) necessary to maintain old growth characteristics. Mature stands were dominated by shrubs that might out-compete tree seedlings and thus did not have old-growth site characteristics.

The two old-growth stands, H.J. Andrews and Trout Creek, both increased in the amount of percent cover in the gaps, and had negligible change in the controls. The biomass trends were also the same for the two sites, though H.J. Andrews had significantly less biomass overall, most likely due to location, such as latitude and climate. The two mature stands responded less similarly in that Martha Creek decreased in the amount of cover for both biomass and percent vegetation cover in the controls sites, while Panther Creek increased slightly in the controls. Both sites increased in biomass and percent vegetation cover in the treatments.

Martha Creek is dominated by *Berberis nervosa*, which may have influenced these results, as is discussed later in the species section.

If increased biomass and diversity is a goal for forest managers, the mature stands in this study did increase in the amount of biomass and the amount of cover and number of species present. However, the species that increased dramatically were weedy and spread rapidly, such as *Rubus ursinus, Epilobium angustifolium* and *Lactuca muralis*, which may exclude tree seedlings from further development.

## 4.3 Within Plot Patterns

Distinct patterns emerge from the contour maps of biomass abundance. H.J. Andrews and Trout Creek, the two old-growth sites, were more patchy than Martha Creek and Panther Creek in both 1990 and 1997, which indicates that pre-treatment conditions may be very important for determining spatial patterns. H.J Andrews and Trout Creek also had the greatest percent change, but the least amount of biomass in 1990. The anomaly of increased biomass in the Martha Creek gap in 1997 is probably due to the inclusion of the gap edges in the calculations.

The great increase of the two old-growth sites is probably due to more space for understory vegetation to grow. The old-growth sites also had more coarse woody debris in the form of snags and nurse logs. Nurse logs and snags may add extra nutrients to the soil and provide shade, which can encourage vegetation growth. This is consistent with findings of Gray and Spies (1997) where tree

seedling establishment was greater on decayed wood in a closed canopy than on the forest floor and that woody debris facilitated tree seedling establishment in exposed areas.

## 4.4 Species Importance

Although average percent change in cover can be calculated for each species, average percent cover changes of most species was site and plot dependent (except for *Rubus ursinus*). Hence, predictability of how understory vegetation will respond to gap creation was very low from these results. This finding is somewhat consistent with the recent findings of Hubbell *et al.* (1999) where spatial and temporal variations in gap disturbance regimes in the Neotropics did not explain variations in species richness, and species composition of gaps was unpredictable.

Nevertheless, species composition was an important variable affecting understory vegetation cover. The understory species that dominated the first seven years of gap response were primarily shrubby species with advantageous dispersal mechanisms, followed by rapidly colonizing herbs and wind-dispersed species. A few species like *Berberis nervosa* and *Vaccinium parvifolium*, were more variable.

Gaps seem to favor shrubs such as *Acer cinncinatum* and *Rubus ursinus*, as shrubs are larger in size and have higher cover values than herbs, though species differed by site. Species with more advantageous dispersal mechanisms, such as rhizomes, stolons or clonal sprouting did better than those without such root

systems. For example, of the four species with an interaction effect between gap and site, three of the species are shrubs that use either rhizomes or stolons (*Gaultheria shallon* and *Rubus ursinus*), or clonal sprouting (*Acer cinncinatum*) for regeneration. In addition, these three species are known to do especially well five to seven years after clear-cut (Franklin 1988).

*Acer cinncinatum* and *Rubus ursinus* both increased in percent cover in treatment sites and behaved much more consistently than *Gaultheria shallon*. This may be because *Acer cinncinatum* can maintain cover by replacing dying aerial stems with new ones from a below ground bud bank. Once established in the understory they will persist for many years (Bailey and Tappeiner 1998, Tappeiner *et al.* 1991). Also, when a tree is felled or falls naturally, aerial stems from vine maple often become pinned to the forest floor and layer, which produces new aerial stems that are likely are likely to increase the extent and density of vine maple clones (O'Dea *et al.* 1995). *Rubus ursinus* is one of the species ubiquitous to newly cut stands and is trailing and rhizomatous, which helps it spread.

Site was not significant for *Gaultheria shallon,* though it was for *Acer cinncinatum* and *Rubus ursinus,* probably due to the great variability of salal at Martha Creek. The response of *Gaultheria shallon* is also interesting because rhizome growth and clonal development are found to increase as overstory density increases in thinned stands in the Pacific Northwest (Huffman 1994, Bailey and Tappeiner 1998). Since gap creation provided more light than before, it is

surprising that salal increased so dramatically at Martha Creek. The other three sites should see an increase in salal as gap closure occurs.

*Berberis nervosa* increased in some gaps and decreased in others, and does not fit neatly into any category. It grows much more slowly than other shrubs, such as salal (Huffman and Tappeiner, in prep, Bailey and Tappeiner 1998), which is consistent with the findings in the gaps. *Berberis nervosa* invasion following disturbance depends primarily on seedling establishment and subsequent slow clonal development (Bailey and Tappeiner 1998), which may explain why *Berberis nervosa* actually decreased in the gaps at Panther Creek and at all the control plots. It also decreased in biomass abundance at the primary plots at Martha Creek. The decrease in biomass in the gap at Martha Creek occurred mostly along the edges where there is greater cover. In addition, field observations of Gray (personal communication 1998) suggest that some *B. nervosa* plants replaced splayed leaves with erect sun leaves, which leads to less cover and biomass. *Vaccinium parvifolium* also decreased in gaps at Trout Creek. This decrease may be attributable to other species such as *Vaccinium alaskanse* out-competing or capitalizing on a similar niche, especially since *Vaccinium parvifolium* increased at other sites.

The three herbaceous species, *Achlys triphylla*, *Linnaea borealis* and *Cornus canadensis,* all increased significantly in the treatments overall, and increased slightly in the controls overall. None of these species were found at Martha Creek, a mature site. *Achlys triphylla* increased in both the controls and

gaps at Panther Creek, and slightly at Trout Creek, while *Cornus canadensis* increased the most in the gaps at Trout Creek, an old-growth site. H.J. Andrews, the other old-growth site, had negligible response for *Achlys triphylla* and *Cornus canadensis* and a slight in crease in the controls for *Linnaea borealis*. Although darker light conditions in old-growth control sites should tend to favor the herbs, rather than the light loving shrubs with advantageous dispersal mechanisms, *Achlys triphylla* was the only herb to significantly increase in the controls. The site response differences of the herbs may be due to competition by shrubby plants or differences in site quality, such as soil nutrients, water holding capacity, micro-topography (Beatty 1983), elevation, aspect or light availability.

Gaps greatly increased cover by weedy species, although total areas affected were less than expected. The controls were not affected by the weedy species. *Epilobium angustifolium* and *Lactuca muralis*, the two weedy species, only appeared in gaps. When looking at percent average cover, the results do not truly express the great increase of weedy species occurrence. A better indicator for weedy species is the frequency of percent cover change for species occurrence which showed an increase by 2000% of the two weedy species. Both weedy species may be starting to decline as weeds are most abundant immediately after gap creation an tend to decline as shrubs and tree seedlings become established 5-7 years after gap creation and shade out the weeds (Franklin 1988).

## 4.5 Species Dominance and Diversity

The dominance-diversity model was only partially supported in this analysis. Understory vegetation at H. J. Andrews, an old-growth site, fits the dominance/diversity model because it had high diversity in 1997 and low vegetation cover values. Martha Creek also fit the model well in that it is was mature site with low diversity, especially in 1990, and high cover values in both 1990 and 1997. Trout Creek is more of an anomaly since it is old-growth site with low diversity, but high cover values, especially in 1997. Panther Creek is also an anomaly since it has high diversity and moderate dominance in both 1990 and 1997. These two sites might be unique due to location, which might lead to increased diversity, or stand age- Panther Creek might actually be older than Martha Creek or Trout Creek may be younger than H. J. Andrews.

Gap creation affected the dominance/diversity of individual species by increasing the dominance of shrubs, as well as increasing the diversity of herbs. The species with the top rankings in the mature sites were *Berberis nervosa, Gaultheria shallon* and *Acer cinncinatum*, which all have advantageous dispersal mechanisms. Tree seedlings and moss both rank in the top three species at H.J. Andrews and Trout Creek. Both of these life forms are more likely to be found in old-growth sites than mature sites as they require more moisture, and sometimes more shade (as is the case for *Tsuga heterophylla*). *Tsuga heterophylla*, a tree species often indicative of old-growth forests, was the third most dominant species

for H. J. Andrews and seventh most abundant at Trout Creek. This supports both Franklin and Dyrness' (1972) climax concept for old-growth, as well as findings by Gray (1995) that *Tsuga heterophylla* seedlings grow better in shady, old-growth sites, rather than mature sites with more light.

In the next seven years tree seedlings will continue to grow in the old-growth sites, and tree seedlings like *Pseudotsuga menziesii* will grow in the mature sites. As these trees grow, they may shade-out some of the more aggressive shrubs. Herbs that are able to tolerate increased shade will flourish, while light loving weedy species will most likely disappear.

# 5. CONCLUSION

Gap creation (treatment) increased average percent cover of understory vegetation in gap centers compared to gap edge. This increase was greatest in the old-growth sites. Gap edges decreased for the most part, except for an increase at H.J. Andrews.

Vegetation cover and biomass increased more in gaps than in controls, though the amount of increase varied by site. The gap at the primary in Martha Creek provided one exception, which was probably due to the inclusion of gap edges in biomass data. Pre-treatment conditions play an important role in determining vegetation change. Stand age class did not help determine the amount of increase for a given site. However, age class did prove important in terms of biomass patterns: old-growth stands were patchier than mature stands, which can be attributed to pre-treatment conditions that include coarse woody debris.

There is a biological legacy of understory species in that vegetation cover of most species increased with gap creation due to greater availability of resources such as light and moisture. Species with advantageous dispersal mechanisms (such as rhizomes, stolons, or clonal growth) increased in cover and biomass more than seed dispersed species in some cases, but species' responses were often site specific. *Berberis nervosa* was the most variable species in that it both increased and decreased. *Rubus ursinus* was the consistent, and increased in all gaps. Weedy species increased more in treatments than in controls, but the actual amount of

coverage per gap was less than expected. Species' dominance was greatest at Martha Creek, a mature stand, and species' diversity was greatest at H. J. Andrews, an old-growth stand. However, the other two stands did not fit the dominance-diversity model due to outside variables.

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